THE EDGE OF A SPECIES' RANGE:

SURVIVAL AND SPACE-USE PATTERNS OF RACCOONS

AT THE NORTHERN PERIPHERY OF THEIR DISTRIBUTION

A Thesis

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By

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ABSTRACT

The raccoon (*Procyon lotor*) is a species that has likely benefited from environmental conditions that followed European settlement of North America. As such, the raccoon has experienced vast range expansion during the past century, moving northward across the continent. However, little is known about the factors that currently govern the northern distribution and the ecology of raccoons at the northern edge of its range. Thus, I studied the population dynamics and social ecology of raccoons in southern Manitoba during spring, summer, and autumn, 2002-2005.

To understand how intrinsic and extrinsic factors affected population dynamics, I examined how winter severity, body condition, age, and gender influenced over-winter survival of raccoons. Winter severity (measured by temperature and snow accumulation) was the most important factor influencing survival (β = 1.08, 95% CI = 0.99-1.17). Over-winter survival estimates ranged from 0.51 (95% CI: 0.41, 0.75) during the harshest winter to 0.84 (95% CI: 0.71, 0.97) during the mildest winter on record for Manitoba. There was no apparent relationship between autumn body condition and autumn food indices and no correlation between autumn and spring body condition. Adults experienced higher survival than yearlings while males had a greater chance of dying compared to females. Variation in abundance natural food items thought to be important during autumn hyperphagia are likely overwhelmed by the presence of grain as an alternative food source, as autumn body condition was constant across all years and plateaued at ca. 20% body fat. I conclude that changes in climatic conditions will likely have the greatest impact on raccoon demographics, with milder winters leading to higher survival.

I also examined the spatial ecology of raccoons to determine if spacing behaviour could limit population growth and to test hypotheses regarding social tolerance and the formation of male coalition groups. Female home ranges were regularly spaced throughout the study site, with minimal spatio-temporal overlap among adult females. However, there where instances where females did display tolerance among conspecifics as well as the ability to partition areas of overlap to use them dissimilarly. While females were generally non-gregarious, plasticity in social tolerance likely precludes spacing behavior from regulating densities of this population. Male social behavior was more complex than previously described for northern populations; most adults (ca. 80%) formed a coalition pair with another male. There was little overlap among male groups and high overlap within groups. The dynamic interaction tests confirmed association in movements for male dyads. Male coalition groups formed despite females being regularly spaced, which contradicts working hypotheses of mechanisms explaining grouping behavior in male carnivores. I propose that group formation occurred because of the benefits that dominant males received through increased efficiency in territory maintenance and the increased likelihood of territory inheritance by subordinate males.

ACKNOWLEDGEMENTS

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1. GENERAL INTRODUCTION

1.1 POPULATION DYNAMICS AND THE EDGE OF A SPECIES RANGE

Understanding factors that influence the distribution and abundance of animals is a necessary and important component of population biology (Caughley et al. 1988, Krebs 1994). Population dynamics are influenced by numerous factors that can be classified as biotic and abiotic (Cappuccino 1995). These factors can be further subdivided into three categories: (1) a factor whose level cannot be modified by the individual (such as climate or the presence of den structures--Caughley et al. 1987, 1988), (2) a factor whose use by one animal reduces the amount available to others within the population (e.g. food abundance or availability of den sites--Andrewartha and Birch 1984, Caughley et al. 1988) and (3) a factor whose effect is influenced by the density of con-specifics (e.g. disease--Caughley et al. 1988, Focardi et al. 2002). As such, the limits to species distributions are circumstantial to the properties of the surrounding environment as well as the physiological abilities of the animal (Caughley et al. 1988). Knowledge of how these various factors interact to influence population demographics can provide insight into how we might expect a population to respond to stochasticity within those variables (Caughley et al. 1988, Fisher et al. 2003). Not only can these factors influence the population biology of a species, but they can also influence social behavior (MacDonald 1983). Resource dispersion and the ability to depreciate resources play an important role in determining territoriality as well as associated and non-associated group formations in carnivores (MacDonald 1983, Johnson et al. 2001). At the edge of a species range, one or multiple resources are limiting, which in turn affect the life history traits and population demographics (Caughley et al.1987, 1988). Identifying these factors

and how they alter the ecology of a species is fundamental to understanding the limits to species distributions (Caughley et al. 1988, Krebs 1994).

1.2 RANGE EXPANSION, SPACE USE, AND SURVIVAL OF RACCOONS

The raccoon (*Procyon lotor*) is a generalist omnivore that evolved in Central America where most procyonids are currently found (Gehrt 2003, Larivière 2004). The raccoon is the only member of the family Procyonidae that has a distribution encompassing temperate regions of North America (Gehrt 2003). During the past century, the raccoon has extended its range into the prairies and parklands of Canada, with the northern edge of its distribution reaching the southern edge of the boreal forest (Larivière 2004). Pristine landscapes historically supported a less diverse predator community composed mostly of small-size specialists such as the black-footed ferret *(Mustela nigripes)*, swift fox *(Vulpes velox)*, American badger *(Taxidea taxus*) and few larger-sized generalists such as grey wolves (*Canis lupus*) and coyotes *(Canis latrans*--Sargeant et al. 1984, Sovada et al. 1995, 2001). Alterations to the landscape following European settlement have influenced the carnivore community leading to an increase in abundance of generalist species (Sovada et al. 2001). Fragmented landscapes now harbor a higher diversity and higher density of mesopredators (Kuehl and Clark 2002, Hunter 1990), especially coyotes, raccoons, red fox (*Vulpes vulpes*) and striped skunks (*Mephitis mephitis*--Sovada et al. 1995, 2001).

Several hypotheses have been proposed for the observed increase in the generalist mesopredator community, including climate change, mesopredator release following the extirpation of larger predators, and increase in availability of anthropogenic food resources. Such hypotheses, however, have not been critically evaluated with empirical data.

Furthermore, little is known about factors that influence the population dynamics of these generalist predators in northern latitudes, such as in the prairie pothole region of Canada (Chafloun et al. 2002). Nevertheless, the change observed in predator community dynamics has had a negative impact for both native ecosystems and human interests (Sovada et al. 2001, Chafloun et al. 2002). For instance, the increased predation rate by mammalian carnivores is the most important proximate factor limiting waterfowl populations (Chafloun et al. 2002). Additionally, the increasing threat of epizootics due to elevated densities of these generalists has garnered public concern and the attention of epidemiologists (Rosatte et al. 2001, State et al. 2005).

As raccoons are a relatively recent invader to the Canadian prairies and parklands (Houston and Houston 1974, Lynch 1971), little is known about their ecology in this new environment. While the first records of raccoons came in the mid 1900s (Soper 1946), their population did not reach significant levels until ca. 30 years ago (Lynch 1971). Even though there was a noticeable increase in raccoon numbers, densities remain much lower than throughout the rest of their distribution (Fritzell 1978, Hasbrouck et al. 1992). Raccoons are prolific in most environments, typically having high survival and high pregnancy rates (Fritzell 1978, Hasbrouck et al. 1992, Fritzell et al. 1985). However, few studies have examined population demographics in the northern edge of their distribution and no studies have examined how survival is influenced by intrinsic and extrinsic factors.

Raccoon space use has also been studied extensively throughout the southern portions of their distribution with social tolerances varying greatly across their range (Walker and Sunquist 1997, Gehrt and Fritzell 1998, Chamberlain and Leopold 2002, Zeveloff 2002). The degree of social tolerance and the formation of aggregations is thought to vary in relation

to resource dispersion (Gehrt and Fritzell 1998), more specifically water resources throughout their southern distribution (Gehrt and Fritzell 1998). At the northern edge of their distribution, home ranges of both male and female raccoons are large while densities remain low, which is likely a function of sparse resources (Fritzell 1978). Depending on the ability to deplete and the dispersion of the limiting resource, we may or may not expect raccoons to maintain exclusive territories. Given the raccoon's large geographic distribution, it represents an ideal species to assess how social tolerances and spatial ecology of a species can vary over large geographic scales.

1.3 THESIS FORMAT AND OBJECTIVES

My overarching objective was to gain insights into the ecology of raccoons at the northern edge of their distribution, to understand how we might expect this population to respond to continued changes in our environment, as well as to address fundamental questions pertaining to social behavior in mammalian carnivores. The thesis consists of five chapters and an appendix, with chapter 2 summarizing field work and methodologies. Chapters 3 and 4 examine survival and spatial ecology of raccoons, respectively. The physiological constraints imposed during winter dormancy are thought to create a bottleneck for northern raccoon populations. Thus, the primary objective of chapter 3 was to assess how various factors influence over-winter survival of raccoons. More specifically, I examined how body condition and winter severity, as well other intrinsic factors interacted to influence raccoon survival. Chapter 4 then focused on social ecology of raccoons. I tested hypotheses regarding social tolerances and group formation. The results are then synthesized in chapter 5 where I discuss the main findings of my research, and ramifications for continued range

expansion and increasing raccoon densities in this area. I also discuss aspects of raccoon social behavior and how this varies spatially across their distribution. An appendix is included, focusing on the usefulness of various techniques used to estimate body condition. These techniques were then used throughout the thesis as a means to estimate body condition.

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2. STUDY AREA AND GENERAL METHODS

2.1 STUDY AREA

Field work was conducted in the Prairie Parkland Region of Manitoba, southeast of Minnedosa (50° 14′ 54″ N, 99° 50′ 30″ W; Fig. 2.1). The area was gently rolling and characterized by an intensively cultivated landscape. Small grain (wheat, barley, oats) and oil crops (mainly canola and flax) occupied much of the study site. Intermixed among agricultural fields were small wooded bluffs, typically ranging in size from 10 to 30 ha, and composed mostly of trembling aspen (*Populus tremuloides*), bur oak (*Quercus macrocarpa),* and choke-cherry trees (*Prunus virginiana*). Numerous wetlands also occurred throughout the area and typically had narrow fringes of vegetation. Several areas managed for upland nesting ducks were also present. These areas were seeded to dense nesting cover and consisted of native warm-season grasses. The predator community was diverse and included raccoons, striped skunks, coyotes, American badgers, red fox, short tailed weasels (*Mustela erminea*) and American mink (*Mustela vison*). Numerous avian predators also occurred including: common raven (*Corvus corax*), American crow (*Corvus brachyrhynchos*), black-billed magpie (*Pica pica*), great horned owl (*Bubo virginianus*), and red-tailed hawk (*Buteo jamaicensis*).

The trapping grid portion of the study site was approximately 78 km^2 (30 $miles^2$) and was bordered by major gravel roads on the east, west, and south sides, and on the north side by Canadian Highway 16. An extensive network of gravel roads divides the interior of the study site.

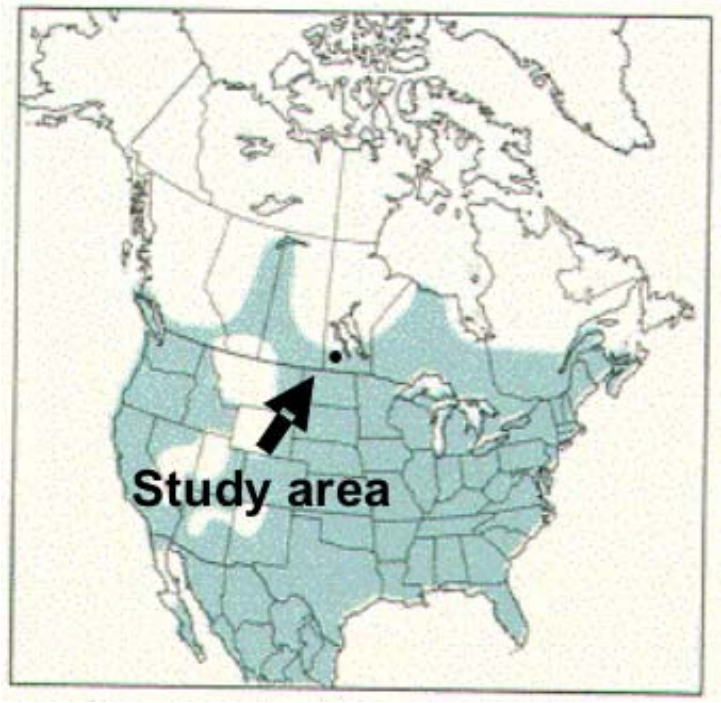

Figure 2.1. North American distribution (shaded area) of the raccoon (*Procyon lotor*) in relation to the location of this study in southern Manitoba, Canada. Figure adapted from Wilson and Ruff 1999. Note that northern spikes in distribution near Alberta/Saskatchewan border extending up to Lesser Slave Lake and at the southern edge of Hudson's bay are errors in distribution map (see Larivière 2004).

2.2 CAPTURE AND HANDLING

I captured 114 raccoons in commercial mesh-wire live traps (Billman Supplies, Columbus, Ohio, USA) during four annual 10-day trapping sessions that occurred in April, May, June, and October from 2002 through 2005. Traps were deployed in a grid fashion and were placed in every quarter section over 30 square miles and baited with canned cat food. Traps were checked each morning as raccoons are primarily nocturnal (Greenwood 1982). All raccoons were anesthetized using a standard dose of 0.20 mg of Zoletil® which was administered to the hind leg (Pitt et al. *in press*). Upon immobilization, raccoons were sexed, weighed, and ear-tagged (National Wing Bands, Newport, Kentucky, USA). Age was determined by examining tooth wear (Grau et al. 1970) and reproductive status was verified by observing size and color of female teats as well as through palpation. Male breeding status was determined by examining size and distention of testicles. All yearling and adult raccoons were equipped with radio collars containing mortality sensors (162-164 Mhz, Advanced Telemetry Systems, Isanti, MN, USA) and released at the site of capture.

2.3 DURATION AND INTENSITY OF STUDY

This project was initiated in April of 2002 when field research commenced and lasted until May of 2005. Raccoons were intensively tracked from early April to early August (2002-2004) and were located on a daily basis. All raccoons previously marked were captured during the third week of April to obtain estimates of spring body condition. Field research was suspended from mid August to mid September. The autumn component of the study was

initiated in mid September and typically continued through the end of October. Most marked raccoons present in the study site were captured during the first week of October to obtain body condition estimates. Following the autumn field component, raccoons were located on a monthly basis from November to March (2002-2005) to assess survival and to identify winter dens.

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3. THE INFLUENCE OF INTRINSIC VS EXTRINSIC FACTORS ON OVER-WINTER SURVIVAL OF RACCOONS AT THE NORTHERN EDGE OF THEIR RANGE

3.1 INTRODUCTION

Understanding the dynamics of animal populations is a fundamental component of ecology (Cappuccino 1995). Survival is an important factor influencing population dynamics, and survivorship itself is affected by both intrinsic and extrinsic factors (Getz 2003). Intrinsic factors are features of individuals, such as gender, age, or body condition (Caughley 1966, Fisher et al. 2003). General patterns of intrinsic mortality are thought to occur in mammalian populations, with yearlings and very old individuals experiencing higher mortality rates compared to mid-aged individuals (Caughley 1966). Additionally, in sexually dimorphic species with polygynous mating systems, males often experience lower survival rates (Promislow 1992). In contrast, survival rates are typically independent of sex in monogamous species with less pronounced sexual dimorphism (Farand et al. 2002).

Extrinsic factors are variables external to the individual and may include climate, parasites, and/or trophic level interactions (Jorgenson et al. 1997, Farand et al. 2002). In northern climates, variation in winter severity is thought to play an important role in shaping population dynamics (Aars and Ims 2002). Understanding the relative importance and contribution of factors that influence survival can provide insight to how we might expect populations to change over time in response to stochasticity within these variables.

The raccoon is a generalist omnivore that evolved in South America and in southern portions of North America (Lotze and Anderson 1979, Zeveloff 2002). During the last several decades, the raccoon experienced unprecedented range expansion, moving northward across the continent and eventually expanding into Canada (Larivière 2004). As such, raccoons are relatively recent invaders to the northern prairie and parkland region of Canada (Lynch 1971, Larivière 2004). However, densities have remained low in this area, suggesting fundamental differences in demographics for raccoons inhabiting this portion of their distribution. Several hypotheses have been proposed for the observed range expansion of raccoons, including increased availability of anthropogenic food resources and climate change (Larivière 2004). While these factors likely interacted in contributing to the success of the raccoon, the variable that has a larger influence over demographics will have direct implications for future changes of northern populations.

At the northern edge of their distribution, raccoons face ecological constraints that are not present in southern latitudes, namely severe winters. To overcome winter severity and associated food shortages, raccoons become inactive during winter (Zeveloff 2002). These bouts of inactivity may last up to 5 months during which raccoons consume little or no food (Mech et al. 1968). To survive such periods, raccoons experience hyperphagia in the autumn to build fat reserves which are then used to meet the metabolic demands incurred during winter dormancy (Zeveloff 2002), when raccoons can lose up to 50% of their body mass (Mech et al. 1968). While this represents an extraordinary physiological adaptation to this environment, it could also represent a bottleneck for the population in terms of viability (Zeveloff 2002).

During hyperphagia, raccoons rely on seasonally abundant food resources to build fat reserves, largely from berry and mast production where these food items are available (Giles 1939, Schoonover and Marshall 1951, Whitaker and Hamilton 1998). Production of these food items is highly variable from year to year and generally follows a boom and bust cycle (Inman and Pelton 2002, Costello et al. 2003). During years of mast production failure, raccoons experience malnutrition and lower survival rates (Zeveloff 2002, citations therein). However, in areas of intensive agriculture, raccoons also rely on grain as an important component of their diet (Greenwood 1982). Grain is a relatively abundant food source in agricultural areas and is generally thought to be a non-diminishable food item (Baumgras 1943). However, the role of grain in building autumn fat reserves remains unknown, but reliable access to grain may negate variations observed in natural food items. If this were true, I would predict that raccoons would have relatively constant fall body condition estimates across years. This assumes raccoons have an upper physiological limit in ability to store body fat, which is common for resident northern mammal populations (Millar and Hickling 1990, Humphries et al. 2003). Furthermore, if autumn condition was relatively constant, I would expect that winter severity (defined as a combination of temperature and snow depth) would dictate the heterogeneity observed in spring body condition as well as explain variations observed in over-winter survival (model B, see Fig. 3.1). Conversely, if raccoons relied largely on natural food items during hyperphagia and grain was a poor substitute, I would predict that autumn body condition would vary annually and in relation to autumn food indices. As such, I would expect to see a strong interaction

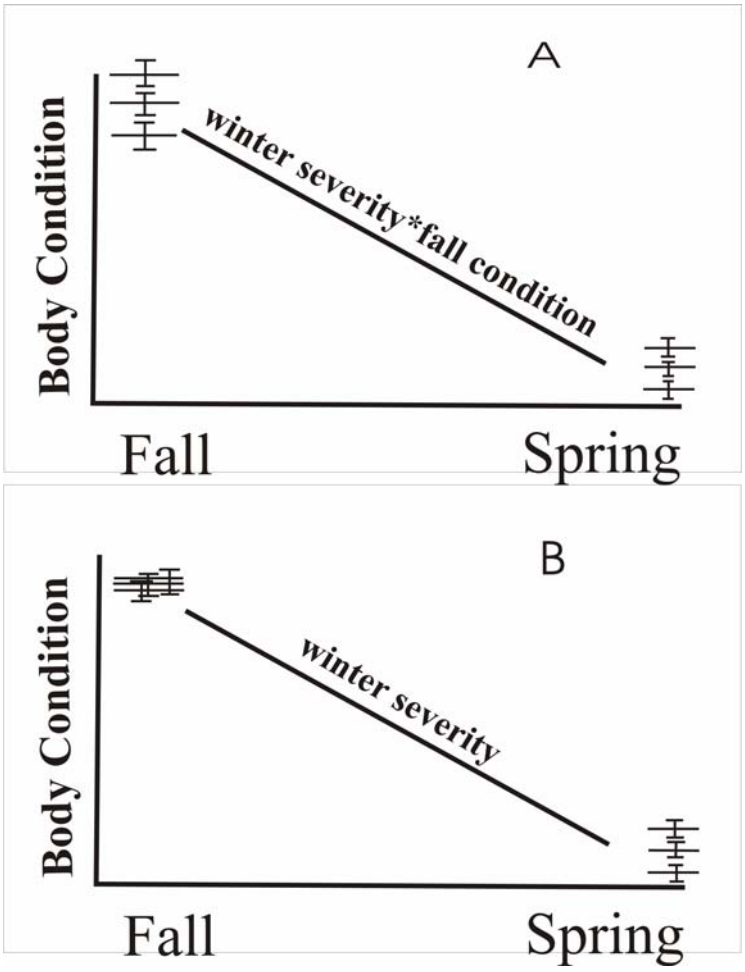

Figure 3.1. Conceptual models of raccoon body condition decline over the period of winter dormancy. Model A (upper) depicts a system which natural autumn food items are an important factors that influence autumn body condition and creates annual variation in this parameter. As such, the decline in body condition that occurs during winter dormancy is influenced by both autumn condition and winter severity. Thus, I would predict that both autumn condition and winter severity would explain heterogeneity observed in over-winter survival as well as the spring condition in which raccoons emerge. Model B (lower) depicts a system which anthropogenic food resources negate variations observed in natural food items, creating relatively constant autumn body condition estimates across years. As such, I would predict the main determinant of spring body condition and over-winter survival to be winter severity as well as weak connectivity between autumn and spring condition.

between autumn condition and winter severity in deterministic models of over-winter survival, as well as strong connectivity between autumn condition and the spring condition raccoons emerge in (model A, Fig. 3.1).

Here, I report the effects of winter severity and body condition on over-winter survival of raccoons. Under model A, I would expect both winter severity and autumn body condition to have a large influence in creating year to year variations in population demographics. Under this model, variation in food resources would significantly impact population dynamics and milder winters alone would not necessarily result in positive shifts in population demographics. Conversely, if autumn condition was relatively constant across years (model B), I would assume that access to grain may negate natural variations observed in food resources and thus I would predict that winter severity and shifts in climatic patterns would have a greater influence in creating changes in population demographics.

I also tested predictions regarding survival patterns observed in mammalian systems for gender and age-specific mortality rates. Raccoons are sexually size dimorphic, have a polygynous mating system (Gehrt and Fritzell 1997, Pitt et al. *submitted*), and males maintain exclusive territories in order to secure access to females (Pitt et al. *submitted*). In such systems, males may experience lower survival rates due to costs incurred during the growth phase or costs associated with reproduction (male-male competition--Clutton-Brock et al. 1982). As such, I predicted that raccoons would have a gender-specific survival rate with females having higher survival than males (even though this pattern of mortality has not been consistently described for raccoon populations--Zeveloff 2002, Chamberlain et al. 1999). I also predicted that raccoon

survival rates would fit general age related patterns observed for mammals, with adults having higher survival rates than yearlings (Caughley 1966).

3.2 MATERIAL AND METHODS

3.2.1 *Capture and handling*

Raccoons were captured during the primary trapping sessions that were held on an annual basis (see chapter 2). Subsequently, it was necessary to capture raccoons a minimum of bi-annually to obtain body condition estimates in the spring and autumn. All estimates of individual body condition were obtained within a period of 10 days, with the period of capture kept constant across years to standardize any temporal effects within or among years.

3.2.2 *Body condition*

Body condition was assessed using bioelectrical impedance analysis (BIA, Kushner 1992). This method relies on the electrical properties of biological tissues and is dependent on a tight inverse relationship between body water and body fat (Kushner 1992, Speakman 2001). A plethysmograph machine was used to run a current of electricity (<1 ohm) through the animal in order to assess resistance and reactance values and morphometric measurements were recorded (see Pitt et al. *in press*). BIA was validated for raccoons and was capable of providing estimates of total body fat as well as lean dry mass and total body water (Pitt et al. *in press*). For my purposes, body condition is defined as percent total body fat. I considered raccoons that were captured in two trapping periods; spring (April 20-April 30) and autumn (October 1-October 10).

3.2.3 *Winter severity and food indices*

I calculated a winter severity index (WSI) using archived weather data from Environment Canada (modified from DelGiudice et al. 2002, Farnes 2002). I added the number of days during which the temperature dropped below -15°C from 1 November to 31 March as well the number of days with 15+ cm of snow accumulation for that same time period. All days were summed and divided by the total number of months.

Autumn food indices were calculated for both choke-cherries and bur oak acorns. Ten racemes from 60 choke-cherry trees were surveyed annually for a total of 600 racemes per year. I established sampling plots, marked, and re-sampled the same trees during the subsequent year to minimize genetic variation constant among years. The ratio of flowers that produced fruit to the total number of flowers per raceme was used as the index of production.

Bur oak acorn production was assessed from 10 woodlots with 10 trees from each plot surveyed annually. Acorn density was measured in 1 m square plots (acorns/m^2) approximately 2 m from the base of the tree. Four plot measurements in each cardinal direction were taken for a total of 400 plots per year. Plots and trees were kept constant across years to minimize natural variation in production among trees.

3.2.4 Data analysis

A multivariate Cox proportional hazard model was used to examine the individual influence of extrinsic and intrinsic variables on explaining heterogeneity observed in over-winter survival of raccoons through a set of *a priori* selected covariates: winter severity, body condition, gender, and age. The proportional hazards model is useful when event times are staggered, such as time to death in this case. Data were both right

and left truncated and I assumed all individuals captured throughout autumn trapping to be present and alive on September 15 of each year, with the winter survival period ending on March 30 for a 195-day survival period. I only included individuals captured during the autumn trapping period.

In the proportional hazards model, the cumulative survival function S*(t)*, which defines the probability of surviving longer than time *t* (assessed in days), is expressed as a hazard function. This is the derivative of the survivor function over time, which is the instantaneous probability of death:

$$h(t) = dS(t)/dt$$

The hazard function is a measure of the potential for the event (in this case death) to occur at a particular time *t,* given that the event did not yet occur. Larger values of the hazard function indicate greater potential for the event to occur. The proportional hazard model given as:

$$h_i(t) = h_0(t)e^{(ß1x1, + ß2x2 + \ldots + ßpxp)}$$

Where $h_i(t)$ is the hazard for the i^{th} case at time t, $h_0(t)$ is the baseline hazard at time t; which measures the potential of an event independently of the covariates. When summed to the entire time interval, the base line hazard is equivalent to a left and right truncated Kaplan-Meier survival estimate (Kaplan and Meier 1958). The baseline hazard is dependent on time; however the covariates are constant across all data points.

Additionally, e is the base of the natural logarithm, and $ß_i$ to $ß_p$ are regression coefficients, and x_i to x_p are model covariates (Cox 1972, Cox and Oakes 1984)

Akaike's Information Criterion (AIC) was used to select the model that optimized goodness of fit and parsimony (Burnham and Anderson 1998). Due to small sample size I elected to use a modified criterion to compensate for this, AIC_c. Models with ΔAIC_c values ≤ 2.0 were averaged across similarly parameterized models and unconditional standard errors were calculated for model averaged coefficients. In total, there were 16 candidate models. All analyses were conducted using SPSS (Version 13.0, SPSS Inc., Chicago, IL, USA).

As supportive evidence to the above methods, I also used analysis of variance to determine if autumn and spring body condition estimates varied among years within seasons as well as with gender and age. I used annual estimates of winter survival to examine the relationship between winter survivorship, winter severity, and autumn body condition. For this analysis, I calculated Kaplan-Meier survival estimates using the Pollock staggered entry design (Kaplan and Meier 1958, Pollock et al. 1989). I considered all raccoons that were present on 15 September as detected by radio telemetry. I also examined the relationship between autumn food indices and autumn condition estimates.

3.3 RESULTS

A total of 114 raccoons (102 M, 85 F; 109 adults, 78 yearlings) were captured from 2002 to 2005 and I obtained 187 estimates of body condition during the spring (n = 115) and autumn (n = 72). Results from Cox proportional hazards models identified seven models

with significant support ($\Delta AIC_c < 2.0$) which accounted for 0.96 of Akaike weights (Table 3.1). All top seven models carried a component of winter severity, with the top model including both winter severity and body condition (Table 3.1). The averaged regression model for winter survival was expressed as:

$$h(t) = h_o(t)e^{[1.08WSI - 0.48condition + 0.42gender + 0.16age]}$$

The final averaged model included all variables made available for inclusion, all of which differed from zero (Table 3.2). Winter severity was the parameter that carried the largest coefficient with a beta value of 1.08, with increasing winter severity associated with decreasing survival. The winter severity beta value was more than twice as large as that of any other covariate. The next most influential parameter was body condition, with individuals that had greater percent body fat having higher survival (Table 3.2). I also observed gender and age biased survival rates, with females having a lower chance of dying ($\beta = 0.42$) while yearlings were at greater risk of mortality ($\beta = 0.16$, Table 3.2). Most mortality (> 80%) took place after day 120 which coincided with the end of January (Fig. 3.2).

Table 3.1. Akaike information criteria rank and weights of models derived from Cox proportional hazard function for winter survival of 72 raccoons in southern Manitoba, Canada, September to March 2002-2005. All models with a ΔAIC_c value < 2.0 were averaged. I provide the estimatable number of parameters (k), loglikelihood value, AIC corrected for small sample size (AIC_c), and the Akaike weights (ω_i) for each model.

Parameters	k	loglikelihood	AICc	ΔAICc	ω_i
WSI, Condition	4	140.30	289.20	0.00	0.22
WSI	3	141.64	289.64	0.44	0.17
WSI, Condition, Gender, Age	5	139.51	289.94	0.73	0.15
WSI, Age	4	140.98	290.56	1.36	0.11
WSI, Condition, Gender	5	139.84	290.59	1.39	0.11
WSI, Condition, Age	5	139.88	290.67	1.47	0.10
WSI, Gender	4	141.17	290.95	1.74	0.09
WSI, Gender, Age	5	140.77	292.44	3.24	0.04
Condition, Age	4	172.97	354.54	65.34	0.00
Gender	3	178.47	363.29	74.09	0.00
Condition, Gender	4	177.89	364.38	75.17	0.00
Condition	3	179.20	364.75	75.55	0.00
Gender, Age, Condition	4	178.46	365.51	76.31	0.00
Age	3	183.65	369.11	78.21	0.00
Null model	2	187.35	374.69	85.49	0.00
Gender, Age	3	186.95	380.26	91.06	0.00

Table 3.2. Model-averaged coefficients (β) of the seven top AICc models (ΔAICc < 2.0) of the Cox proportional hazard function for winter survival of 72 raccoons in southern Manitoba, Canada, September to March 2002-2005. Model coefficients with 95% upper (95UCI) and lower (95LCI) confidence intervals estimated from unconditional standard errors are provided.

Parameter	β	95%LCI	95%UCI
WSI	1.08	0.99	1.17
Condition	-0.48	-0.59	-0.37
Gender	0.42	0.17	0.67
Age	0.16	0.07	0.23

*WSI defined as winter severity index

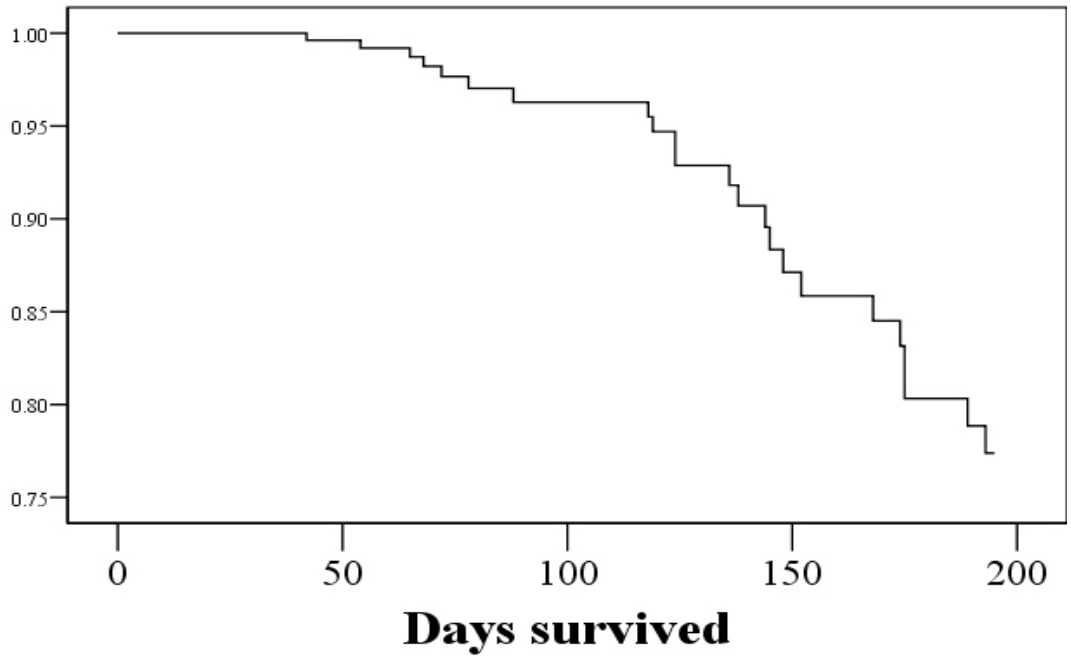

Figure 3.2. Hazard function estimated at mean values of covariates for Cox proportional hazard model results from 72 raccoons in Manitoba, Canada, 2002-2005 from September 15 to March 31 each year for a 195 day survival period.

Body condition of raccoons was greater in the autumn (20.5 $\pm$ 0.7%) than in the spring (11.2 $\pm$ 0.3%, $F_{1,165} = 68.7$, $P < 0.001$). Body condition estimates of raccoons varied annually ($F_{2,165} = 7.0$, $P < 0.001$). However, autumn body condition estimates were similar across years (Fig. 3.3, Tukey test: range 1.3-1.4, P = 0.29-0.33); albeit large annual variation in natural food indices (choke-cherries: $F_{1,598} = 6075$, $P < 0.001$; acorns: $F_{1,798} = 3384$, $P < 0.001$; Table 3.3). I observed no apparent relationship between autumn body condition and the spring condition of raccoons (Fig. 3.3). At the population level, autumn body condition appeared to have no relationship to annual estimates of over-winter survival of raccoons with the year with the highest over-winter survival corresponding with the autumn of the lowest mean estimate of body condition (Fig. 3.4).

Spring body condition varied among years ($F_{2,165} = 7.0$, $P = 0.001$; Fig. 3.3) with post hoc Tukey test identifying the spring condition estimates of 2002 and 2005 being different from 2003 and 2004 estimates (Fig. 3.3). Raccoon mean spring body condition decreased with increasing winter severity (Fig. 3.5). Winter survival, as estimated by Kaplan-Meier staggered entry, ranged annually from 0.51 ($\pm$ 0.18, 95% confidence limit) to 0.84 ($\pm$ 0.13, 95% confidence limit; Table 3.4). Winter survival decreased as winter severity increased (Fig. 3.6). Similar to the Cox regression, we also observed a difference in body condition among gender ($F_{1,165} = 18.4$, $P < 0.001$), with females having more body fat. Likewise, we observed an age effect, with older individuals being in better condition than yearlings ($F_{1,165} = 3.9$, $P = 0.02$).

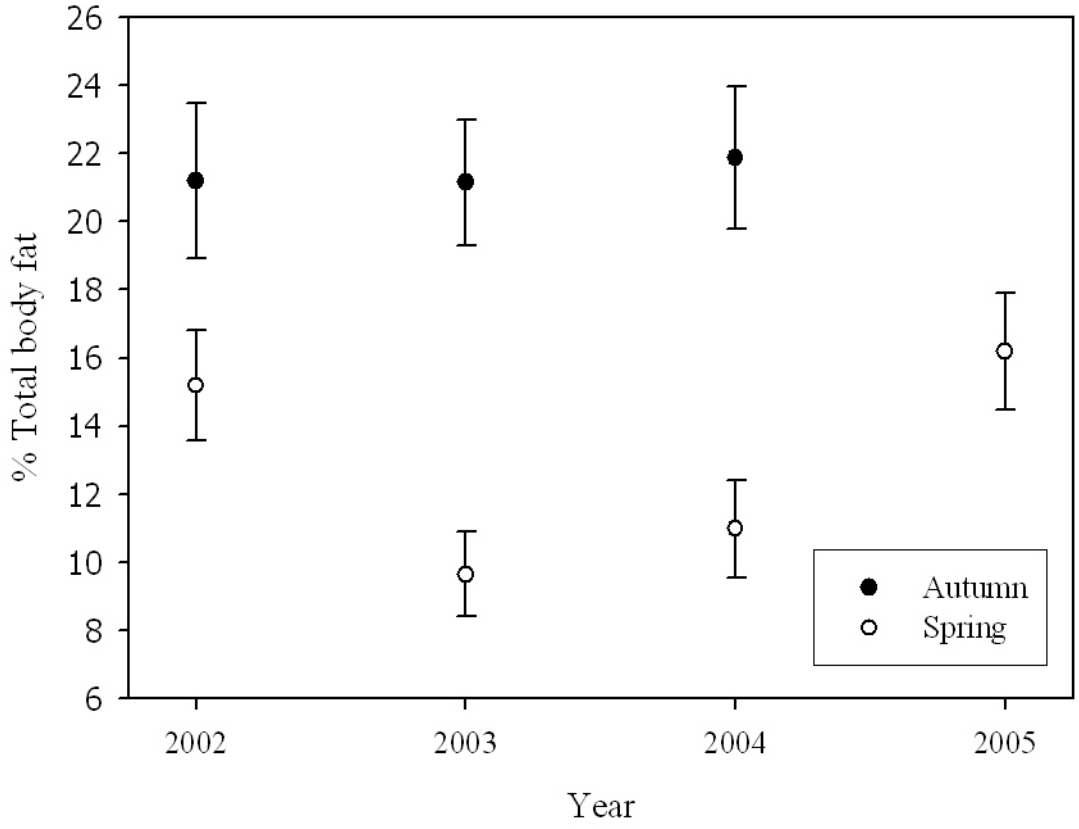

Figure 3.3. Mean spring and autumn body condition (% total body fat ± 95% confidence interval) for 114 raccoons in Manitoba from 2002-2005.

Table 3.3. Autumn body condition (Autumn percent total body fat, TBF) of raccoons and food indices for berry (proportion of fruit produced per raceme of choke-cherries) and mast production (density of bur oak acorns in 1-m^2 plots) in southern Manitoba from 2002-2004. All values are $\pm$ 95% confidence intervals.

Year	Autumn TBF	Choke-cherries	Acorns
2002	20.3 $\pm$ 3.2 (*n=21*)	----	---
2003	20.8 $\pm$ 2.0 *(n=22)*	0.58 $\pm$ 0.10	65.3 $\pm$ 8.2
2004	21.1 $\pm$ 2.1 *(n=29)*	0.13 $\pm$ 0.07	8.1 $\pm$ 1.8

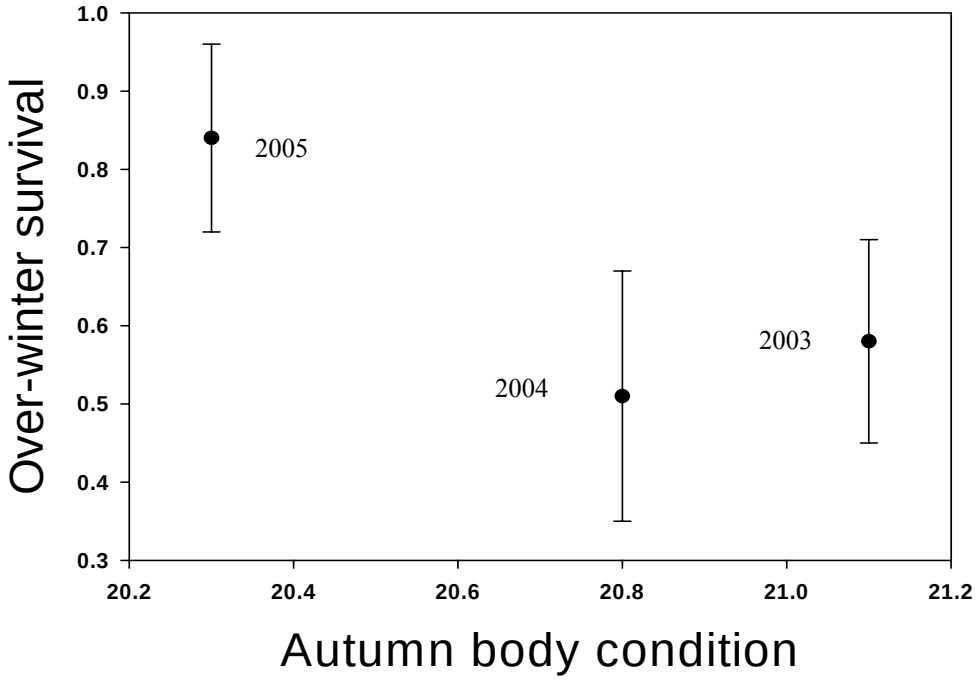

Figure 3.4. Relationship between over-winter survival rate and autumn body condition (mean percent total body fat with 95% confidence limits) for 114 raccoons in Manitoba, Canada, 2003-2005.

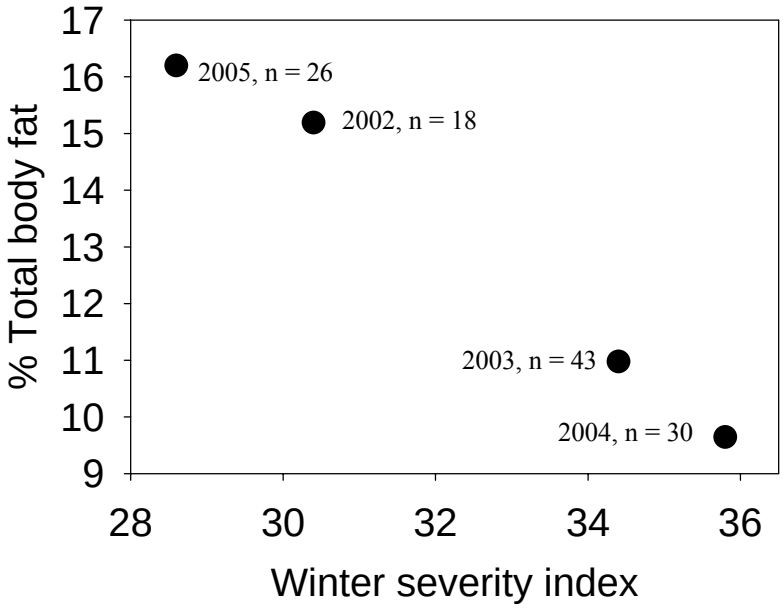

Figure 3.5. Relationship between mean spring percent total body fat and winter severity index for 114 raccoons in Manitoba, Canada, 2002-2005 (year and sample size given next to each point).

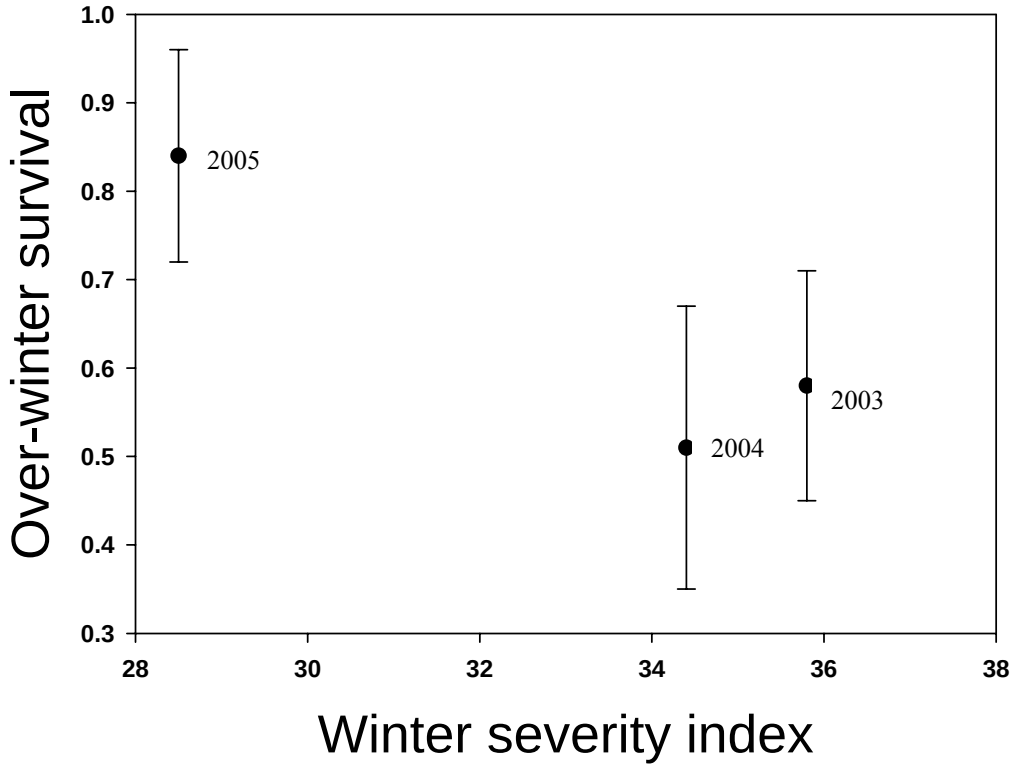

Figure 3.6. Relationship between over-winter survival ± 95% confidence intervals and winter severity index for 114 raccoons in Manitoba, Canada, 2003-2005.

Table 3.4. Mean spring body condition (Spring TBF*) ± 95% confidence intervals, over-winter survival (S) ± 95% confidence intervals, and pregnancy rates (proportion of radio collared females pregnant) of raccoons in Manitoba, Canada, 2002-2005 relative to winter severity indices (WSI**).

Year	WSI	S	Spring TBF	Pregnancy Rate
2002	30.1	---	15.2 ± 1.3	0.20
2003	34.4	0.58 ± 0.15	9.6 ± 1.7	0.32
2004	35.8	0.51 ± 0.18	11.0 ±1.5	0.55
2005	28.5	0.84 ± 0.13	16.2 ± 1.8	0.83

*TBF = total body fat

**WSI = winter severity index as measured through temperature and snow accumulation

3.4 DISCUSSION

The edge of a species' range marks the point where, on average, the contribution of an individual to the next generation is about unity (Caughley et al. 1988). Understanding the relative importance of factors that influence survival at the edge of a range can provide insight into how we might expect that population to respond to stochasticity within those variables (Caughley et al. 1987, Fisher et al. 2003). Given the successful range expansion of raccoons following European settlement and their ability to exploit resources in altered landscapes (Larivière 2004, Prange et al. 2004), there has been an interest across several facets in understanding how raccoon demographics in this portion of their distribution will continue to change. For example, the realization that the mitigation of waterfowl nest predation requires an understanding of predator ecology has led to renewed interest in predator population dynamics (Larivière and Messier 1998, Chafloun et al. 2002). Given the generalist nature of the raccoon, it undoubtedly plays an important role in waterfowl nest predation and changes in their demographics are of interest to waterfowl managers (Chafloun et al. 2002).

Additionally, the increasing threat of raccoon rabies spreading westward across the continent has led to several initiatives to employ oral rabies vaccine programs in Canada and across the eastern United States (Rosatte et al. 1998, 2001, State et al. 2005). Effective delivery of such programs requires an *a priori* knowledge of both the spatial and population ecology of the species of interest (State et al. 2005). Changes in densities have important ramifications for both the deployment of such programs and for the ecology and spread of the virus. Thus, understanding how climate and other intrinsic and

extrinsic factors influence the survival of northern mammal populations, such as raccoons, has important applications and ramifications (Humphries et al. 2002, 2003).

My results support the notion that in polygynous mating systems, where males and females are sexually dimorphic in body size, gender-specific mortality rates are observed (Clark et al. 1989, Promislow 1992). While not all studies of raccoon demographics have found that females have higher survival than males (Chamberlain et al. 1999, Gehrt and Fritzell 1999), my results do suggest that, in northern populations, males are more susceptible to mortality. In polygynous mating systems, males typically have larger home range sizes and higher movement rates compared to females (Gehrt and Fritzell 1997). Additionally, due to sexual dimorphism, males and females experience differential growth rates (Isaac 2005). Because males have faster growth rates, less energy is devoted to fat storage for winter energy expenditure. These combined factors are hypothesized to be the underlying mechanisms contributing to the observed differences in survival rates (Clutton-Brock et al. 1982, Zeveloff 2002). These differences in life history traits are likely magnified at the edge of a species range; and have also been described for other northern carnivore populations (Hwang et al. 2005). Additionally, a general pattern of age-related mortality exists for mammals, with an increase and then decrease in survival as a function of age (Caughley 1966). I was only able to partition my data into yearling and adult age classes, but still detected an age-related difference in survival with adults experiencing higher over-winter survival. Higher adult survival rates may be due to differences in winter den site selection or differences in body composition among age classes (Hwang et al. 2005, Pitt et al.

submitted). However, both gender and age are relatively constant variables with little ability to create long-term shifts in survival rates of raccoons.

Conversely, factors such as food resources, body condition, and winter severity show much more temporal plasticity and have a greater ability to create stochasticity in population demographics (Mech et al. 1968, Zeveloff 2002, Humphries et al. 2003). While food is an important component to any system, my results indicate that food and the ability to store body fat had little influence in explaining heterogeneity in over-winter survival of raccoons. Moreover, I observed weak connectivity between autumn and spring body condition, with the condition raccoons entered in the autumn explaining little of the variation in the spring condition of raccoons. Even though I observed large differences in autumn food indices, autumn body condition did not vary among years supporting the predictions of model B.

In contrast, I did find a strong relationship between winter severity (as measured through temperature and snow cover) and over-winter survival. Proportional hazards model of over-winter survival identified winter severity as the variable with the greatest impact on over-winter survival of raccoons. Additionally, there was a strong inverse relationship between winter severity and spring body condition. Many resident northern mammals have a threshold of ca. 30-40% maximum body fat storage (Humphries et al. 2003). Raccoons in this study averaged ca. 20% body fat, with very few individuals attaining 30% body fat. This level of fat accumulation is relatively low for winter dormancy and demonstrates that raccoons are not fully adapted physiologically for adequate fat storage in this relatively new portion of their distribution. For species with nominal physiological adaptations for winter dormancy, spring condition and survival

becomes a function of duration and temperature deficit incurred during the period of inactivity (Humphries et al. 2002, 2003); which appears to be the case for this population.

In terms of absolute values of survival, I observed large differences across years. In 2003 and 2004 the survival estimates were among the lowest reported in the literature for raccoons, with only ca. 50-55% of raccoons in the study site surviving. In contrast, Manitoba experienced one of its mildest winters on record in 2005 and accordingly I observed a significant increase in survival ($S_{(t)} = 0.84$), which was in parity with what would be expected for a healthy population of similar-sized carnivores (Zeveloff 2002). Additionally, milder winters resulted in female raccoons emerging in better spring condition, in turn resulting in a positive relationship between pregnancy rates and winter severity. Pregnancy rates for adult females ranged from 20 to 55% during the normal winters observed, but 83% of females became pregnant after the mild winter of 2005. Female raccoons are capitol breeders and fat reserves are essential to support energy requirements during this metabolically expensive period where little food is consumed (Zeveloff 2002). Likely, the costs incurred during more severe winters influenced female body condition such that they were not able to invest in reproduction.

Assessing the differential effects of individual variables on survival is a fundamental component of understanding animal population dynamics (Lebreton et al. 1993). Recent studies have highlighted the need to understand how changes in climate-mediated energetic constraints will influence the density and distribution of mammals (Humphries et al. 2002, 2004). Regardless of the mechanism that has contributed to climate change over the past century or in the future, we do know that the continent is experiencing milder temperatures and is predicted to receive less precipitation

(Humphries et al. 2003, citations therein). Both of these variables were included in our index of winter severity. Furthermore, the greatest factor contributing to heterogeneity observed in over-winter survival of raccoons was winter severity. Theoretical and empirical models of the effects of climate change on resident northern mammal populations predict both positive and negative species dependent effects (Humphries et al. 2004). Species that are highly physiologically adapted to northern environments could be negatively influenced by warmer temperatures (Humphries et al. 2002, 2004). However, the raccoon is a non-native generalist which likely does not possess any advanced physiological adaptations. Thus, as the continent continues to experience milder winters due to warmer temperatures across the Canadian prairies, there likely will be direct positive shifts in raccoon population dynamics and further range expansion into northern areas.

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4. SOCIAL ORGANIZATION AND GROUP STRUCTURE OF RACCOONS AT THE NORTHERN EDGE OF THEIR DISTRIBUTION

4.1 INTRODUCTION

Understanding factors that govern spatial organization and social interactions is a fundamental pursuit in animal ecology (Adams 2001). Space use and spatial patterns are influenced by the distribution of resources as well as the presence and characteristics of other individuals (Shier and Randall 2004). Males and females commonly exhibit varying spatial patterns due to differences in fitness pressures among genders (Lott 1991). Typically, female space use is influenced by resource dispersion and requirements. However, male space use is coupled with the ability not only to exploit these same resources, but also to mate with females. As such, male spatial patterns also become a function of female spatial distribution (Macdonald 1983).

Territory ownership is a major determinant of fitness in territorial animals (Morrell and Kokko 2004). Social tolerance within both genders should be linked to resource availability, as defense of territories costs energy and should only occur if a net gain results (Davies and Houston 1984, Maher and Lott 2000). Territorial defense would not be beneficial if 1) the resource of interest is spread thinly over a large area that cannot compensate for cost of defense and 2) the resource is overly abundant and not worth defending (Krebs and Davies 1993, Samson and Huot 2001). Conversely, it has been hypothesized that grouping behavior and aggregations are favored when resources are highly concentrated. If the resource is not easily depleted, the benefits accrued to defend this resource would not be worth the cost of defending, meaning we would expect

aggregations of individuals with static interactions that do not necessarily have positive dynamic interactions[1] (see Doncaster 1990). As male spatial organization is a function of female dispersion in many mammalian systems, it has been hypothesized that female spatial organization may be the main determinant of sociality in adult male carnivores (Caro 1994). As females attain localized high densities, a male's ability to successfully monopolize access to a female's home range decreases (Gehrt and Fritzell 1998). As competition among males increases, the benefits of forming coalition groups becomes greater (Caro 1989, 1994). In such instances, we would expect positive dynamic interactions among males that cooperatively defend these resources while maintaining mutually exclusive territories between groups.

The raccoon is an omnivorous carnivore that has a distribution that spans most of North America (Zeveloff 2002). Raccoon space use and social organization has been studied extensively throughout the high density/southern latitude portion of its distribution. It has been demonstrated that the raccoon has the ability to display a wide array of social tolerances, ranging from completely tolerant, to strict territoriality, to complex systems of associated and non-associated aggregations (Walker and Sunquist 1997, Gehrt and Fritzell 1998, Chamberlain and Leopold 2002, Kamler and Gipson 2003). Ecological factors, such as resource dispersion may in part explain this variability observed across the species' distribution (Zeveloff 2002).

The raccoon is known to have a high affinity for water and its associated resources (Lotze and Anderson 1979, Gehrt and Fritzell 1998), and it has been hypothesized that female spatial dispersion in portions of its range is dictated by the

[1] *Static interaction* is defined as the spatial overlap of two home ranges and congruence in at least some part of their utilization distribution of location data while *dynamic interaction* is the dependency in the simultaneous movements of a pair of individuals (see Doncaster 1990).

dispersion of water resources (Gehrt and Fritzell 1998). When this resource becomes limiting and aggregated in the landscape, females respond by becoming aggregated, causing localized high densities (Gehrt and Fritzell 1998). This aggregation of females has been hypothesized as the underlying mechanism dictating the recently discovered formation of male coalition groups in south Texas and Mississippi raccoons (Gehrt and Fritzell 1998, Chamberlain and Leopold 2002). Male coalition groups have positive dynamic interactions and maintain exclusive territories to other male groups (Gehrt and Fritzell 1998).

At the northern edge of the raccoon's range distribution, both male and female home ranges are large while densities remain low, which is likely a function of sparse resources (Fritzell 1978a). However, in the prairie parkland region of North Dakota and Manitoba, both wetland densities and water resources are relatively abundant indicating that these may not be the limiting resource selected for. Depending on the ability of raccoons to deplete local resources and the dispersion of the limiting resource, we may or may not expect females to maintain exclusive territories. It has been hypothesized that raccoons are limited at the northern edge of their range distribution by access to anthropogenic food resources as well as access to suitable den sites (Greenwood 1981, Larivière 2004), both of which can be found on farmsteads. Additionally, farmsteads have previously been described as highly selected resources for northern populations of raccoons (Fritzell 1978b) and other prairie carnivores (Larivière and Messier 1998).

Essentially no comprehensive study has examined spatial patterns and social interactions of raccoons outside of their southern distribution. Studies of northern populations in the 1960s and 1970s were typically unable to assess more than a few

individuals, only marked a select subset of captured individuals, and generally were unable to link spatial and temporal interactions at the population level (Sharp and Sharp 1956, Mech et al. 1968, Schneider et al. 1971). However, these studies provided some evidence of a system of mutual avoidance among raccoons, including females (Mech et al. 1968). The most recent, thorough spatial study of northern raccoons occurred in North Dakota, where no more than two adult females and four adult males were monitored in any given year (Fritzell 1978a). Adult males appeared to remain solitary and maintained exclusive territories that typically overlapped with two or more females. However there was anecdotal evidence that males temporarily interacted (Fritzell 1978a). Only in one year were two female close enough to have overlapping home ranges and one individual was a yearling and the other was an adult (Fritzell 1978a). Based on this single observation it was reported that parous or pregnant females occupied extensively overlapping home ranges (Fritzell 1978a), a notion which has persisted in the literature (Zeveloff 2002). Conversely, if females did maintain exclusive territories, it may be possible that raccoons are self regulated by spacing behavior, which would explain the consistently low density observed in the prairie and parklands of Canada.

Here, I report on the spatial organization and social interactions of raccoons to test hypotheses regarding both female and male social behavior and discuss this in the context of social regulation as well as the formation of male coalition groups in relation to south Texas raccoons (Gehrt and Fritzell 1998). As resources are scarce, I hypothesized females would maintain relatively exclusive home ranges dispersed in a regular pattern. Additionally, since male grouping behavior has been hypothesized to be a result of female aggregations, I expected males to maintain exclusive territories and remain

asocial. Alternatively, if females are aggregated in the landscape, I would expect males to form coalition groups to cooperatively defend territories and access to females as found in the southern part of their range (Gehrt and Fritzell 1998, Chamberlain and Leopold 2002).

4.2 METHODS

4.2.1 *Capture and radio tracking*

I tracked through nighttime telemetry 104 radio-collared raccoons which were captured during annual trapping sessions that occurred from 2002 to 2004. Trapping effort was extensive, with a total of 4800 trap nights per year occurring during this time span over the 78 km^2 study site. Raccoons were radio tracked from approximately 1900 to 0600 hours each night from mid April to the end of July using a truck mounted null peak system (Spencer et al. 1987).

4.2.2 *General spatial analyses*

Locations were obtained by triangulation with a minimum 2-hour interval between successive fixes to insure independence of data (Salvatori et al. 1999). At least three directional bearings of an individual were used to estimate its location with each bearing generally taken within 5-8 minutes of each other to reduce telemetry error (White and Garrott 1990). Personnel were equipped with global positioning systems (GPS) to obtain the coordinates and the bearing of the vehicle. I calculated the standard deviation of the bearing error (Lee et al. 1985) and used the standard deviation to calculate 95% confidence ellipses in program LOCATE II (Nams 1990). Locations were determined in Universal Transverse Mercators (UTMs) using the maximum likelihood estimator available in LOCATE II software. These data were entered into program ArcView 3.2®

Geographic Information System (GIS) Software (Environmental Systems Research Institute, Redlands, California, USA). Home ranges were estimated using the animal movement extension in ArcView (Hooge and Eichenlaub1997). I calculated 100% minimum convex polygons (MCP) to estimate home ranges which were used for all spatial analyses. However, I also provide 95% adaptive kernel estimates of home ranges for comparison purposes, and estimated 50% core home ranges using both MCP and adaptive kernel methods.

I tested for correlation between number of locations and range size using Pearson's product moment to determine if there was a relationship between sampling effort and estimated home range size (Larivière and Messier 1998). Area observation curves were also created to determine the number of locations required to accurately depict the home range without being biased by sample size (Odum and Kuenzler 1955). All values are reported as mean $\pm$ standard error unless stated otherwise.

4.2.3 *Nearest neighbor analysis*

To assess the spatial distribution of home ranges within the study site I used the Clark-Evans ratio of arithmetic centers to determine the distance of each raccoon from other conspecifics using the following equation (Clark and Evans 1954):

$$[\bar{x} - E(\bar{x})]/SE(\bar{x})$$

The expected distance $[E(\bar{x})]$ and its standard error were determined using corrections which accounted for both edge effects and correlations among nearest neighbor distances using the following equation (Donnelly 1978, Sinclair 1985):

$$E(\bar{x}) = 0.5\sqrt{A/n} + (0.051 + 0.041/\sqrt{n})L/n$$

where *n* is the number of observed points (arithmetic centers in this case) and *A* is the area for which *n* points fall, and L is the length of the boundary of the region (Donnelly 1978). Standard error was calculated using the equation:

$$SE(\bar{x}) = \sqrt{0.07A + 0.037L\sqrt{A/n}}/n$$

Clark-Evans ratios (R) range in value from 0 to 2.15, with 0 indicating maximum aggregation, 1 indicating a random distribution, and 2.15 representing perfect uniformity or a regular pattern (Clark and Evans 1954). If raccoons were territorial I would expect home ranges to be uniformly distributed within the study site; conversely, if I found high social tolerance I might expect to see aggregations of individuals. This analysis was used as one line of evidence for describing socio-spatial patterns of raccoons, while also using it to test hypotheses regarding male group formation and for comparison with studies of raccoons in high density portions of their range.

4.2.4 *Static interaction*

Static interaction in animal movements is defined as the spatial overlap of two home ranges and congruence in at least some part of their utilization distribution of location data (Doncaster 1990). For first approximation of static interaction, I report the inter- and intra-sexual percent overlap of home ranges. Overlap area was calculated in ArcView using the merge and intersect functions in the Xtools extension (DeLaune 2003). As this

measure of socio-spatial interaction does not take into account the utilization of the shared areas, I also examined the correlation in home range use of each range using a grid cell method of analysis. I used Spearman's rank correlation coefficient which was calculated on the pairs of fix scores obtained from all of the grid-cells frequented by one or both animals, and then tested for correlation in use between the two utilization distributions (Doncaster 1990).

Home range overlap indices were also calculated to determine intensity of use for raccoons with adjacent overlapping home ranges. Association was quantified by using the modified ratio presented by Ginsberg and Young (1992) in the equation:

$$[(n_1 + n_2) / (N_1 + N_2)] \times 100$$

where n_1 and n_2 relate to the number of locations that occur in the area of overlap and N_1 and N_2 refer to the total number of locations for that individual.

4.2.5 *Dynamic interaction*

To assess temporal interactions among raccoons that shared portions of overlapping home ranges, I used a non-parametric test using simultaneous telemetry locations in program DYNAMIC (Doncaster 1990). The dynamic interaction test was used to determine if movements of two raccoons that were monitored simultaneously were moving independently of each other by determining if the two animals were located within a critical distance more or less often than expected by chance (Doncaster 1990). I constructed cumulative frequency histograms for distance intervals separating paired locations that would be expected if animals were moving at random as well as the actual

observed distance between locations. I then determined if the observed distance of simultaneous paired locations differed from the expected frequency. A distance of 100 m was used to classify temporally paired locations following Gehrt and Fritzell (1998). If the observed frequency distribution of locations that fell within the critical distance were greater than what I would have expected by chance, it was considered a positive interaction indicating that the movement of the two animals was positively associated. Conversely, a significant negative interaction occurred if the expected frequencies (unpaired locations) were greater than the observed (paired) frequencies for each distance interval. The use of the dynamic interaction test was employed only if the observed area of overlap was at least 20% of the individual's home range. A Chi-square test was used to determine whether a positive or negative dynamic interaction had occurred with all tests considered significant at $\alpha = 0.05$. I coupled this test with denning data obtained concurrently throughout the study to determine if individuals that were associated with each other during nightly activity were also selecting daytime resting sites with the same conspecific, this being supportive evidence for positive dynamic interactions.

4.3 RESULTS

4.3.1 *General space use*

I calculated 105 (58 M, 47 F) home ranges of raccoons during the spring and summer of 2002 to 2004 based on 7,705 locations. Mean number of locations used to estimate a home range was 74 (SD $\pm$13). Area observation curves consistently yielded asymptotes near 60 locations per home range which was used as my benchmark for data analyses. Additionally, I found no relationship between home range size and number of locations

($r^2 = 0.08$, P = 0.51, $n = 105$) which indicated home range estimation was not influenced by the number of locations. Minimum convex polygon (MCP) estimates of male home ranges averaged 15.6 $\pm$ 1.5 km^2, which were larger than female home ranges (4.4 $\pm$ 0.4 km^2; $F_{1,93} = 22.7$, P < 0.001, Table 4.1). Similarly, male MCP core estimates of home ranges were also larger than females ($F_{1,93} = 23.7$, P < 0.001). Males that were associated with coalition groups had larger home ranges (22.9 $\pm$ 1.9 km^2) than those that were not (6.5 $\pm$ 0.90 km^2; $F_{1,47} = 12.3$, P < 0.001), while pregnant or parous females tended to have smaller home ranges compared to nulliparous females ($F_{1,38} = 17.3$, P < 0.001; Table 4.1). For each sex, 100% MCP and 95% Kernel estimates of home ranges were similar among years ($F_{2,93} = 0.91$, P = 0.41; $F_{2,96} = 0.27$, P = 0.76, respectively). Similarly, there was no yearly difference in 50% core estimates of home ranges for either MCP of kernel estimates, respectively ($F_{2,93} = 0.42$, P = 0.66; $F_{2,93} = 0.37$, P = 0.69).

Table 4.1. Summary of 105 estimated home ranges and 50% core areas (km^2) for raccoons during the spring and summer in Manitoba, 2002-2004. Home range estimates are provided in both minimum convex polygon (MCP) and adaptive kernel estimates.

		MCP				Kernel			
Sex		100% MCP		50% MCP		95% Kernel		50% Kernel	
Year	*n*	Area	SE	Area	SE	Area	SE	Area	SE
Females:									
2002	12	4.42	0.61	1.21	0.27	4.56	0.89	0.48	0.11
2003	17	4.44	1.00	0.77	0.16	2.91	0.58	0.37	0.09
2004	18	5.34	0.93	1.13	0.31	4.50	0.96	1.03	0.61
All years									
Pregnant	14	2.91	0.43	0.53	0.14	2.05	0.56	0.24	0.06
Non-pregnant	33	5.06	0.55	1.21	0.20	4.74	0.60	0.83	0.33
Total	47	4.42	0.43	1.00	0.15	3.94	0.48	0.65	0.24
Males:									
2002	16	13.33	2.07	4.28	0.82	17.68	3.26	3.12	0.92
2003	24	15.58	2.39	4.52	0.83	19.37	3.43	2.81	0.87
2004	18	17.40	3.32	4.91	1.03	21.75	4.49	2.39	0.46
All years									
Dyad	32	22.93	1.86	6.80	0.69	28.70	2.77	4.12	0.73
Non-dyad	26	6.49	0.90	1.85	0.31	7.50	1.25	1.08	0.22
Total	58	15.56	1.54	4.58	0.52	19.20	2.14	2.76	0.46

4.3.2 *Nearest neighbor analysis*

Female raccoon home ranges were spaced regularly throughout most of the study (Table 4.2). Clark-Evans ratios for females ranged in value from 1.32-1.87, with home range dispersion in one year being only marginally different from a random distribution (Fig. 4.1), but still tended towards a regular pattern (Table 4.2). In 2002 and 2003, female home range dispersion was significantly regularly or uniformly spaced (Table 2). This uniformity in dispersion of female home ranges differs considerably when compared to southern populations of female raccoons, which were found to follow a clumped distribution in all years (Table 2, Gehrt and Fritzell 1998).

Arithmetic center of male home ranges varied from a clumped to random distribution when not accounting for male coalition groups, with Clark-Evans ratios ranging from 0.72-1.14. These values were similar to those presented for Texas raccoons, indicating spatial dispersion of males may be similar in high and low density populations (Table 4.2). However, when I merged male coalition groups and treated them as a single unit, male dispersion tended towards a regular pattern, significantly so in all but one year (2003, Fig. 4.2) which was only marginally significant towards a regular distribution (Table 4.2).

Table 4.2. Spatial distribution of male and female raccoon home ranges in Manitoba, 2002-2004 and south Texas raccoons from 1990-1992 (values adapted from Gehrt and Fritzell 1998). A significant value greater than 1 indicates a uniform or regular pattern, while a value lower than one indicates a clumped distribution. A value not different from 1 indicates a random distribution.

		Female			Male*			Male**	
Year	Season	N	R	P	N	R	P	R	P
Manitoba									
2002	Spring/Summer	12	1.57	< 0.001	16	1.14	= 0.26	1.51	< 0.001
2003	Spring/Summer	17	1.87	< 0.001	24	0.74	= 0.01	1.22	= 0.07
2004	Spring/Summer	18	1.32	= 0.08	18	0.72	= 0.02	1.50	< 0.001
Texas									
1990	Spring	9	0.66	<0.05	8	0.63	<0.05	---	
	Summer	9	0.51	<0.01	8	0.71	<0.05	---	
1991	Spring	13	0.57	<0.01	9	0.43	<0.01	---	
	Summer	13	0.58	<0.01	13	0.44	<0.01	---	
1992	Spring	16	1.10	>0.10	18	0.51	<0.01	---	

*Male dyads treated independently

**Male dyads merged

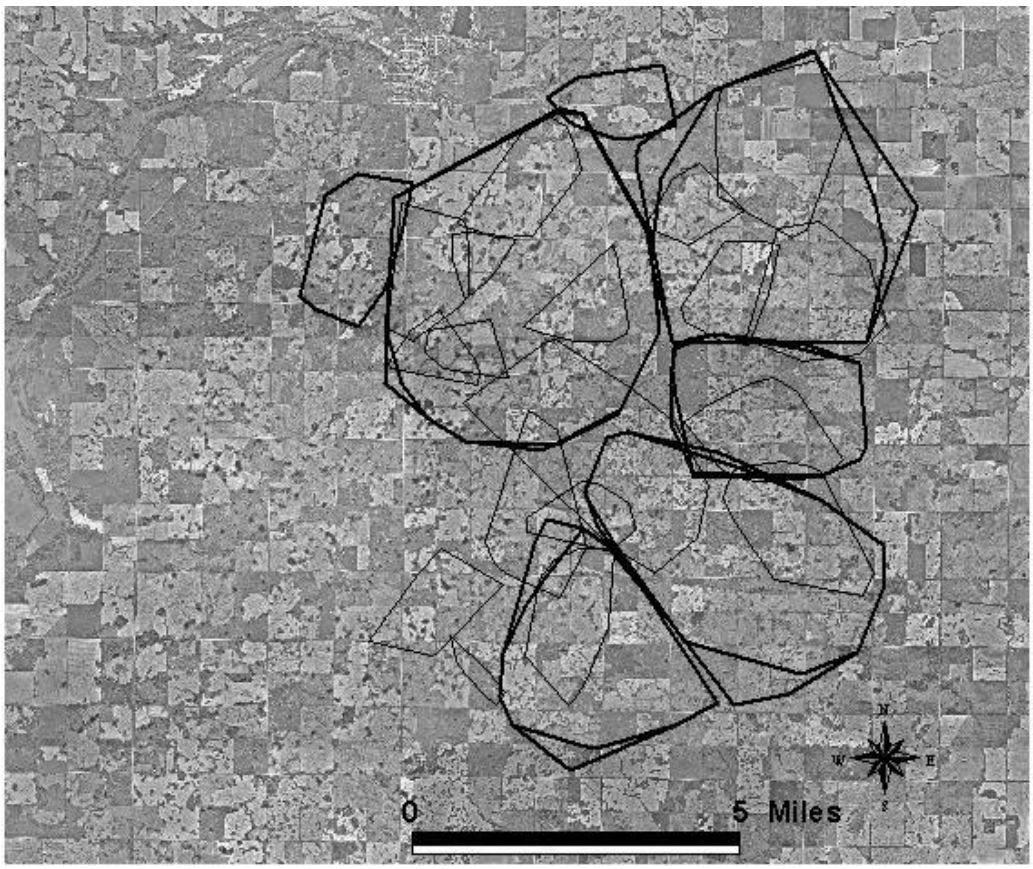

Figure 4.1. Adult male and female home ranges of raccoons in Manitoba from mid April–July, 2004. Dark lines are associated with male home ranges while lighter lines are representative of female home ranges.

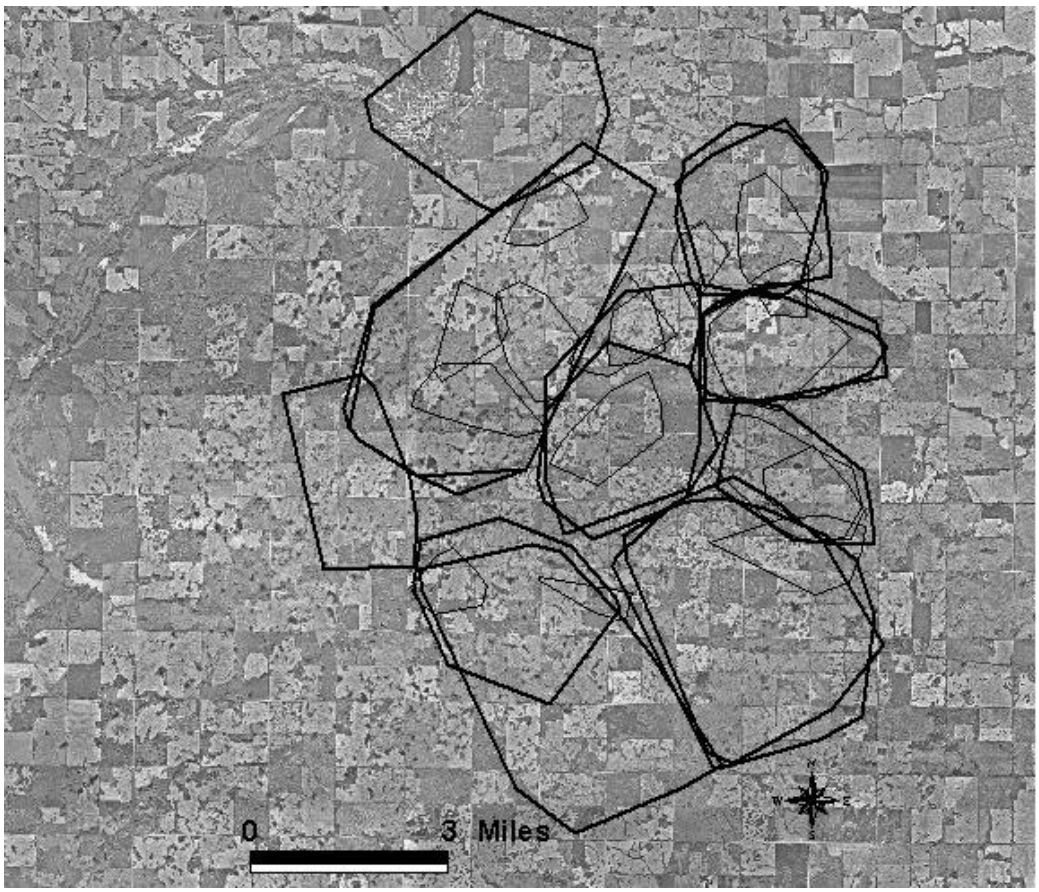

Figure 4.2. Adult male and female home ranges of raccoons in Manitoba from mid April to July, 2003. Dark lines are associated with male home ranges while lighter lines are representative of female home ranges.

4.3.3 *Static interaction*

Among females inhabiting the study site, percent overlap of home ranges (100% MCP) averaged 12 $\pm$ 2 % for all years, and ranged annually from 6-21%. When considering only adult females, percent home range overlap was less ($U = 727$, $n_1 = 58$, $n_2 = 34$, $P = 0.04$), ranging from 2 to 12 % and averaging 5.6 $\pm$ 1.3% (Table 4.3). Home range overlap indices followed the same trends as percent overlap for adults and yearlings, with overlap indices being higher for all females (15 $\pm$ 3 %) compared to adults only (7 $\pm$ 2%). Overlap indices followed no trend of either being consistently lower or higher compared to percent overlap ($U = 1903$, $n_1 = 64$, $n_2 = 64$, $P = 0.59$), suggesting that percent overlap closely approximated intensity of use in these overlap zones as well. Correlation in utilization distributions were typically negative for most females, with mean correlation values ranging from -0.44 to -0.53 for all females. Similarly, when considering only adult females, values were lower, ranging from -0.51 to -0.67 (Table 4.3). These negative values indicate repulsion or dissimilar use in shared utilization distributions. In only one instance did I record a positive association of area utilized by two females and in this case a yearling female was still traveling with her mother during the subsequent year following parturition. However, even though females were typically negatively associated with each other based on nighttime activity locations, I did observe one instance where 3 adult females shared a common maternity den for more than two weeks (Fig. 4.3), but Spearman's rank correlation values for these females were negative: -0.09 ($P > 0.20$, $n = 50$), -0.16 ($P = 0.12$, $n = 50$), and -0.42 ($P < 0.001$, $n = 50$), but significantly so only in 1 case.

Table 4.3. Intra-sexual percent overlap percent, overlap indices, and correlation in utilization distributions (UD) for 105 estimated raccoon home ranges in Manitoba, 2002-2004. Correlation in UD calculations are based on Spearman's rank correlation and all male values are calculated excluding values for dyads.

		Males						Females			
		All males		Within dyads		Among dyads		All females		Adult females	
Year		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
2002	Percent overlap	18.1	3.5	81.6	5.3	0.0	0.0	21.1	8.1	12.5	6.9
	Overlap indices	15.2	2.9	85.3	3.1	0.0	0.0	17.8	9.5	9.2	4.5
	Correlation in UD	-0.38	0.09	+0.78	0.09	0.0	0.0	-0.44	0.05	-0.51	0.07
2003	Percent overlap	22.1	3.8	91.6	1.8	3.2	0.7	17.9	5.1	11.1	4.6
	Overlap indices	16.4	3.3	94.2	2.2	3.1	0.6	23.6	7.4	16.1	6.3
	Correlation in UD	-0.43	0.06	+0.81	0.07	-0.79	0.06	-0.48	0.1	-0.59	0.08
2004	Percent overlap	18.4	4.5	95.5	1.4	2.1	0.3	6.7	1.7	2.2	1.1
	Overlap indices	19.1	5.1	87.3	2.2	3.1	0.6	9.2	2.8	4.9	1.3
	Correlation in UD	-0.62	0.08	+0.84	0.04	-0.84	0.09	- 0.53	0.06	-0.67	0.05

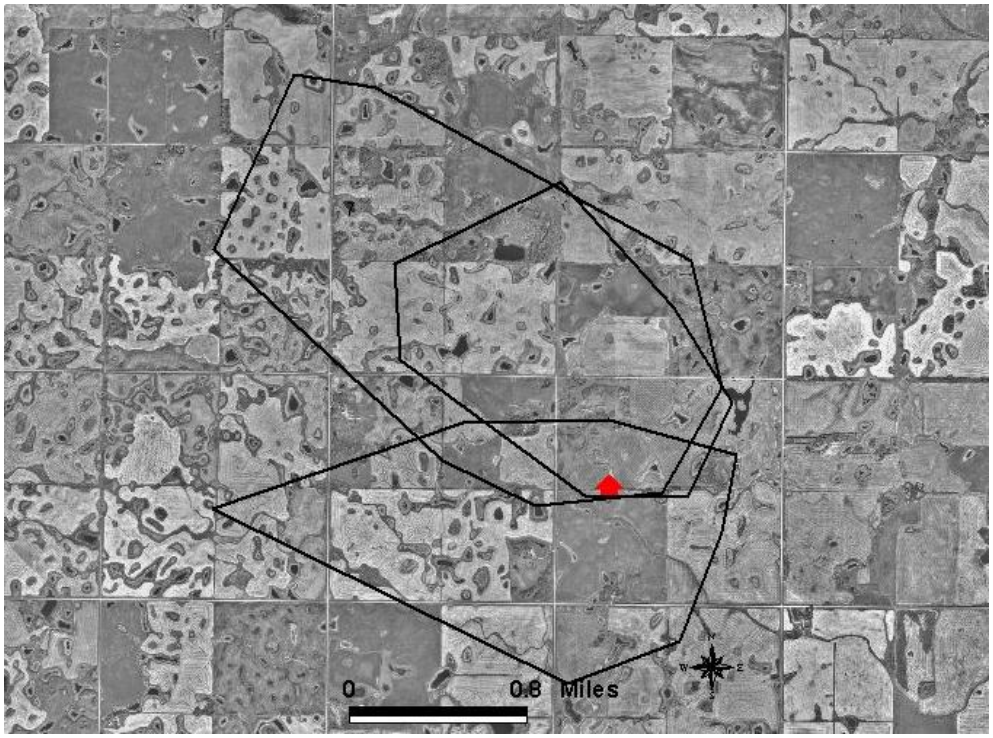

Figure 4.3. Home range (100% MCP) for 3 parous female raccoons that shared a common maternity den (building symbol) in Manitoba during the summer, 2003.

Percent overlap for male home ranges (100% MCP) was 19 $\pm$ 4 %, and ranged annually from 18-22 % when not accounting for coalition groups. Males formed distinct spatial groups (Figs. 4.4 and 4.5) with overlap within these spatial groups being high, ranging from 82-96 % annually. Home range overlap among male coalition groups was low; with percent overlap ranging from 0 to 3 % (Table 3). Overlap indices were similar to values for percent overlap for both among and within male coalition groups (U = 3437, $n_1 = 83$, $n_2 = 83$, P = 0.68), again suggesting that percent overlap was a close approximation of how intensively these shared areas were used. Spearman's rank correlation values were significantly positive for all male coalition groups, with annual values ranging from +0.78 to +0.84 (Table 3), which indicated utilization distributions were used similarly. Correspondingly, significantly negative values were recorded for among coalition group tests (range -0.79 to -0.84). All values were significant past P < 0.001.

Male coalition groups overlaid multiple female home ranges, with female home ranges typically overlapping the primary coalition group they resided in extensively ($\bar{x}$ = 80 $\pm$ 5 %, range 62-100%) and had nearly congruent external boundaries (Figs. 4.1 and 4.2). Female overlap among non-primary coalition groups was negligible ($\bar{x}$ = 6 $\pm$ 2 %). Lone adult males had few known females present within their home ranges and coalition groups secured access to more females ($\bar{x}$ = 2.3 $\pm$ 0.4) than lone males ($\bar{x}$ = 0.5 $\pm$ 0.2), even considering that multiple males were associated with access to these females (U = 16, $n_1 = 30$, $n_2 = 9$, P = 0.001).

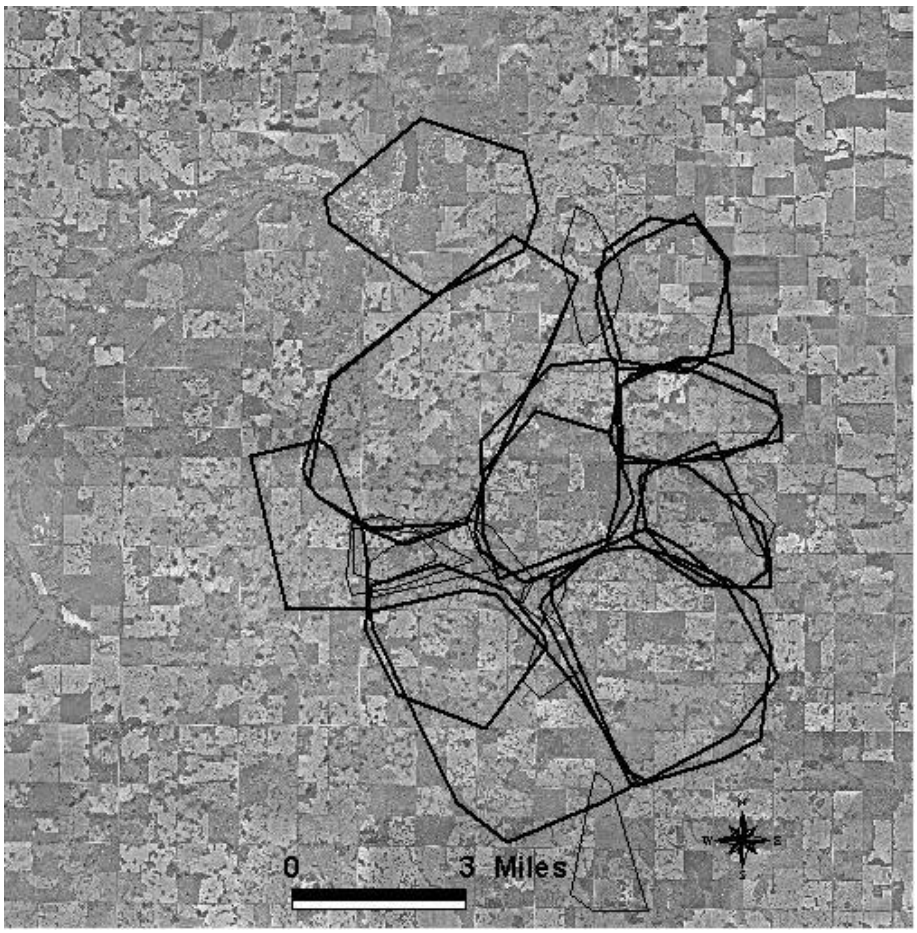

Figure 4.4. Home ranges (100% MCP) of 24 male raccoons in Manitoba, 2003. Dark lines indicate adult males (n = 16) and light lines represent yearling males (n = 8). Note that there are 7 coalition groups that have nearly congruent boundaries.

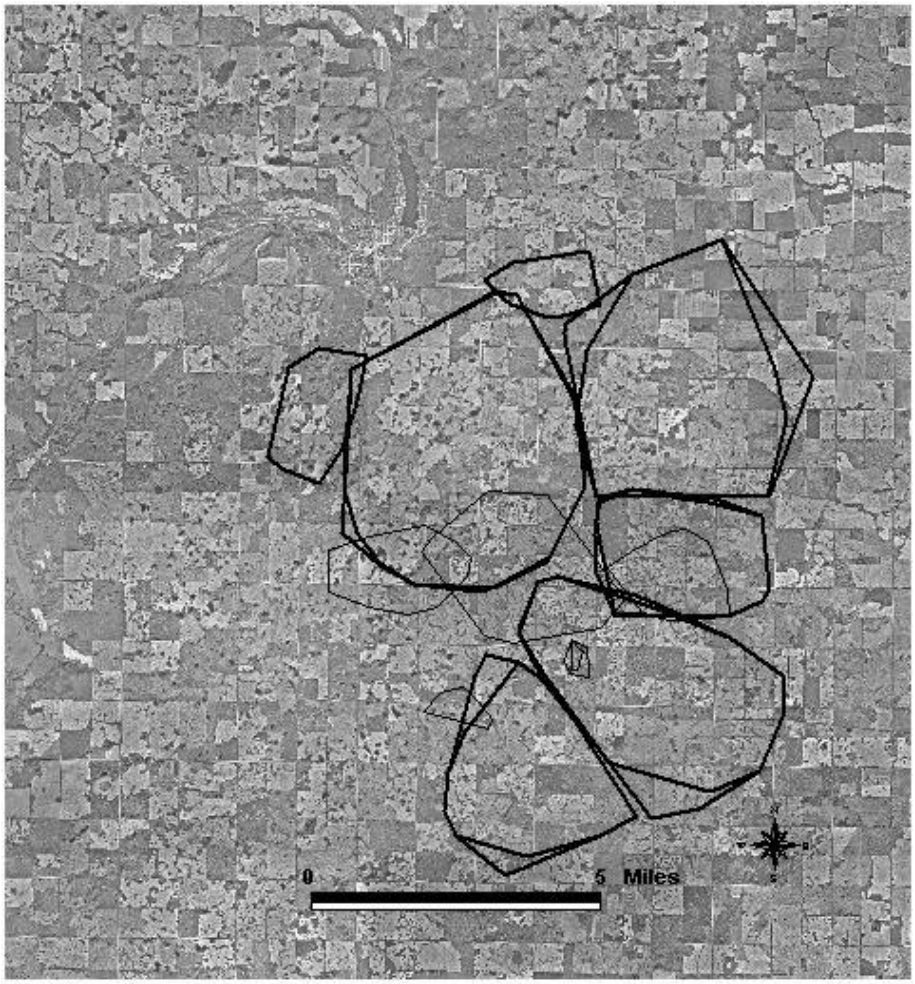

Figure 4.5. Home ranges (100% MCP) of 18 male raccoons in Manitoba, 2004. Dark lines indicate adult males (n = 12) and light lines represent yearling males (n = 4). Note that there are 5 coalition groups that have nearly congruent boundaries.

4.3.4 *Dynamic interaction*

All significant tests for male dynamic interactions were positive (see Fig. 4.6) and I observed no negative interactions among males. All positive tests were significant past the $P < 0.001$ level. I identified 15 pairs of males (3 in 2002, 7 in 2003, and 5 in 2004) that were positively associated with each other and formed coalition groups, with group size never exceeding 2 individuals. Males remained grouped during the entirety of the study and these males were found together at daytime rest sites 93% of the time during spring and summer months and were also found together at winter denning locations. On several instances I also observed paired males at daytime rest locations during the breeding season in the presence of females.

I only observed one instance of a positive interaction among female-female dynamic interaction tests. This was the case noted previously in which a yearling female was still traveling with her mother the year following parturition.

4.4 DISCUSSION

Both male and female home ranges were among the largest reported in the literature, which is consistent with the notion that resources are sparsely distributed at the northern edge of the raccoon's distribution. Home range sizes were similar to previous studies of raccoons in low density portions of their distribution in North Dakota (Fritzell 1978a). Male home ranges were nearly four times as large as female home ranges, which is nearly the same order of magnitude as was found for Texas raccoons (Gehrt and Fritzell 1997). The observed sexual discrepancy in home range size is likely a function of attempts by

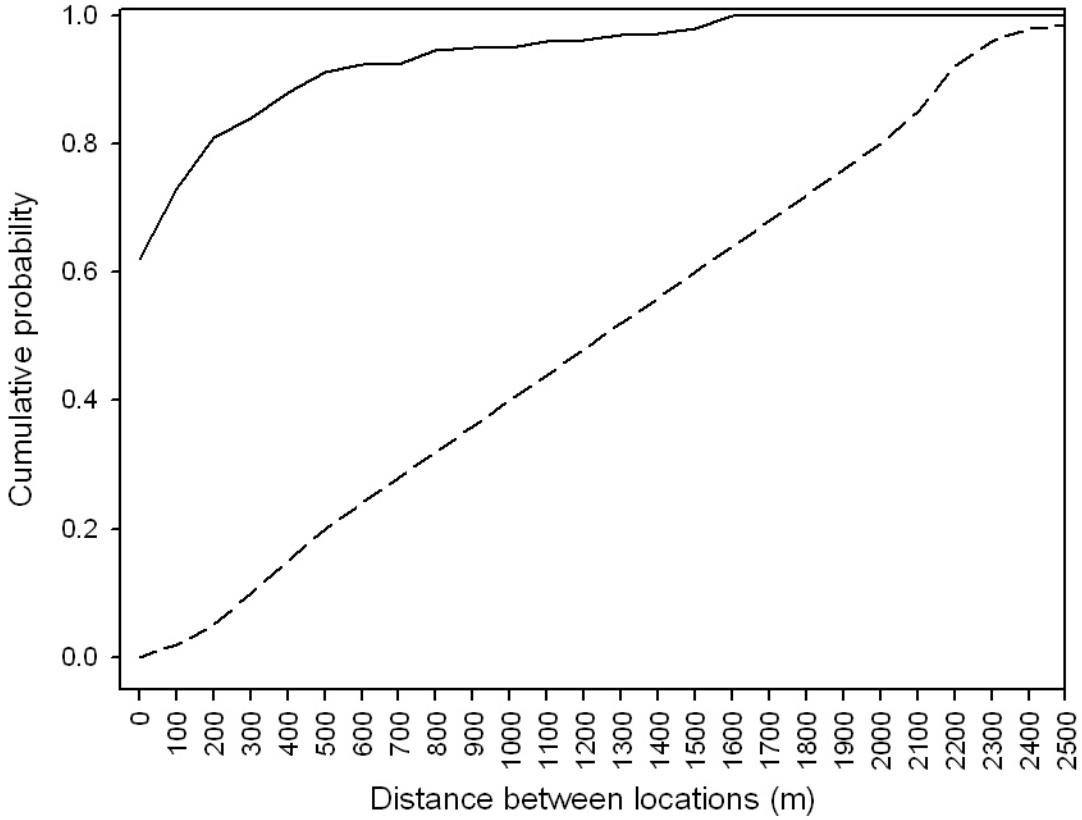

Figure 4.6. Example of a test for dynamic interaction between two adult male raccoons in Manitoba during the summer of 2004. In this case, a positive interaction is indicated by the observed cumulative probability (solid line) being greater than the expected cumulative probability (dashed line).

male raccoons to encompass more females and represents varying fitness pressures between genders (Gehrt and Fritzell 1997).

4.4.1 *Female spacing patterns*

Female home ranges were regularly distributed in our study area. It has been hypothesized that females in particular may have a strong reliance on farmsteads for both food and denning locations at the northern edge of their distribution (Fritzell 1978b, Larivière 2004). However, farmsteads in the study site were randomly distributed ($R = 0.99$, $P = 0.91$), suggesting that this resource alone is not the sole dictator of female home range dispersion in the landscape. Other mechanisms, such as additional resources and/or social tolerances likely play a role in female spatial patterns.

Most studies of spacing behavior and social interactions of raccoons have found that females are typically gregarious and socially tolerant of conspecifics (Walker and Sunquist 1997, Gehrt and Fritzell 1998, Kamler and Gipson 2003). However, no studies detailed spatial organization of females in low density portions of their distribution. In this study, females generally maintained relatively exclusive home ranges to each other, especially when considering adults. When areas were shared, they were used dissimilarly with Spearman's rank values indicating repulsion in most cases. However, tests revealed no temporal segregation within these areas. This may be in part due to the fact that the shared areas were used minimally, meaning there would be no reason for females to temporally segregate.

Spacing behavior has been proposed as a mechanism of population regulation for omnivorous carnivores that maintain low densities, such as black bears (*Ursus*

americanus--Garshelis 1994, Samson and Huot 2001). In these systems, food, predation, and disease appear to play minor roles in population regulation processes. Raccoons have maintained relatively low densities in the prairie parkland region since populations became established (Lynch 1971). Studies of cause-specific mortality have generally only identified mortalities associated with limiting factors (e.g. Fritzell and Greenwood 1984), leaving spacing behavior as a plausible mechanism for population regulation. However, even though females generally maintained exclusive home ranges, there were instances where pregnant or parous females shared extensively overlapping home ranges and also shared common resources thought to be limiting. While it did not occur often, the ability of females to tolerate conspecifics and to use shared areas dissimilarly likely precludes the possibility for raccoons to self regulate their population by spacing behavior, especially at the density levels I observed. Additionally, dispersal was heavily male-biased and most female yearlings remained as residents. However, female dispersal has been hypothesized as a necessary mechanism for regulation by social tolerance (Samson and Huot 2001).

4.4.2 *Male spacing patterns*

Sociality in carnivore systems is rare, with only 10-15% of the 271 species in the family Carnivora forming groups outside of the mating season (Gittleman 1989, Valenzuela and Macdonald 2002). Moreover, even fewer of these spatial groups are comprised of adult males. For instance, in the family Procyonidae, coatis (Genus: *Nasua*) are known to form bands that may exceed 30 individuals (Gompper et al. 1997); however, these bands generally consist of many females and yearling males with typically only one adult male. When male coalition groups do form, it is thought to be related to aggregations of

females (Caro 1994, Gehrt and Fritzell 1998). In studies of male coalition groups in felid social systems, females were either temporally and permanently aggregated and shared extensively overlapping home ranges (Caro 1989).

In this study, I found that most adult males (80%) were positively associated with con-specifics to form coalition groups. These male coalitions were positively associated with each other during both nighttime activity locations and daytime resting sites and maintained exclusive territories to other adult males. Group association endured throughout the year, including breeding season. These findings are contradictory to the notion that male raccoons are asocial in low density portions of their distribution (Fritzell 1978a, Zeveloff 2002). Coalition groups formed despite the fact that females were not aggregated in this study, suggesting this is not a prerequisite for the formation of male spatial groups in raccoons as was previously hypothesized (Gehrt and Fritzell 1998). Thus, the mechanisms and benefits accrued by the formation of spatial groups in raccoons remains unknown.

Both lone males and coalition groups were able to gain access to females, which was similar to results found in Mississippi (Chamberlain and Leopold 2002). However, this was not the case for Texas raccoons where lone males were unable to secure access to females (Gehrt and Fritzell 1998). However, in this study, coalition groups were able to secure access to more females than lone males, even when considering the fact that multiple males were associated with females residing within coalition group home ranges. Additionally, I observed heterogeneity in the number of females that males were able to secure access to within coalition groups, ranging from 1-6 females.

In avian systems, cooperative behavior among male groups has been studied more extensively and three distinct systems have been described with dominate-subordinate hierarchies (Lank et al. 2002, Krakauer 2005). The main differences in these systems are the age of group formation (through attrition or during adulthood), whether or not male coalitions actively defend territories, and the ability of group members to breed. This system reflects group coalitions of *Chiroxiphia* manakins, where it is hypothesized that subordinate males benefit through increased likelihood of future inheritance of the occupied territory (increased likelihood hypothesis--McDonald and Potts 1994). In this system, group formation occurred after adulthood was reached, males were territorial, and subordinate males did not father offspring (McDonald and Potts 1994).

For raccoons, group formation also occurred after adulthood was reached, as opposed to through attrition (Krakauer 2005). There were several instances in this study when following the death of one male, the remaining male re-grouped with another con-specific in the study site. Additionally, I observed instances where the presumably dominant (older) male was eventually overthrown and left the territory and became solitary. The remaining male re-grouped in the same territory with another male that was marked as a yearling the previous year. In systems where group formation occurs through attrition, once a member of a coalition is lost, the remaining male(s) remains solitary (Krakauer 2005). Also following the increased likelihood hypothesis, coalition groups were territorial. However, I was unable to assess if subordinates were able to breed in raccoon coalition groups because I could not assess paternity of offspring, which makes it difficult to assess direct or indirect fitness benefits of group formation. Nevertheless, I propose that in this study, group formation was likely due to the benefits

that dominant males received through increased efficiency in territory maintenance and the increased likelihood of territory inheritance by subordinate males.

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5. SYNTHESIS

The raccoon is one of the most successful mammalian carnivores inhabiting North America. Due to its generalist nature and ability to adapt to changing environments, it has been capable of exploiting a variety of landscapes, from the boreal forest to the prairies, deserts, and even urban areas (Zeveloff 2002, Larivière 2004). The observed range expansion and continued increase in raccoon densities across most of its continental distribution has led to an interest in understanding the mechanisms responsible for these changes as well as an understanding of what factors currently govern the northern limit of their distribution (Larivière 2004). There has been much speculation and *post hoc* data analysis presented in attempts to identify plausible mechanisms, with varying degrees of success (Gehrt et al. 2002, Gehrt and Clark 2003). Such hypotheses examined include: the mesopredator release hypothesis, increased access to anthropogenic food resources, global warming/climatic constraints, decreased trapping pressure, and human introductions (Rogers and Caro 1998, Gehrt et al. 2002, Larivière 2004). However, after closer scrutiny many of these hypotheses appear to receive little support (Gehrt and Clark 2003, Larivière 2004) and there has been little in the way of empirical data collected to evaluate the remaining plausible hypotheses.

In this study, I examined over-winter survival of raccoons to identify how ecological factors influenced this component of population dynamics. I found that winter severity had the greatest impact on over-winter survival. I also found a strong inverse relationship between winter severity and the spring body condition of raccoons. Furthermore, autumn body condition estimates were relatively stable across years, suggesting variation in natural food items had little influence in determining autumn condition. My findings suggest that winter severity is the ecological factor that has the strongest influence on this bottleneck

period of survival and is likely the most important factor currently limiting or constraining their northern distribution. Food abundance appears to have little influence on population dynamics, which is not uncommon among generalist omnivores that are able to exploit a variety of anthropogenic food resources (Prange et al. 2003, 2004).

In his proposed theoretical framework for identifying limits to species distribution, Caughley et al. (1987, 1988) demonstrated that various factors can interact to control the edge of a species range through both ramp (continuous) and step (presence/absence) effects. Thus, multiple factors may have interacted in contributing to the past success of the raccoon. It is my contention that the availability of grain as an alternative food resource likely acted as a step effect which initially contributed to the observed range expansion by raising the latitude at which raccoons could survive by providing a constant and reliable food source which enabled them to cope with temperate climates (Larivière 2004). However, as the northern edge of their distribution moved northward, the ramp effect of winter climatic stresses likely began to be the primary constraint which limited their distribution. Physiological adaptations for living in northern climates, such as the ability to enter torpor or hibernation, are hypothesized to be pleisiomorphic (Geiser 1998). As such, it is unlikely that raccoons have any physiological adaptations besides increased fat storage to cope with winter dormancy. Consequently, I predicted and observed that survival and spring condition should be directly influenced by the duration and temperature deficit incurred during winter dormancy assuming autumn body condition is constant. Furthermore, as we continue to experience milder winters across the Canadian prairies, I would predict that there will be direct positive shifts in raccoon population dynamics.

I also examined the spatial ecology of raccoons to assess how social behavior can vary across its distribution in response to sparse resources and to determine if spacing behavior through female territoriality could influence the population dynamics of raccoons. I found that female home ranges were regularly spaced throughout the study site, with minimal amounts of spatio-temporal overlap among adult females. However, there where instances where females did display tolerance among con-specifics, as well as the ability to partition areas of overlap to use them dissimilarly. While females were generally non-gregarious, the ability to show plasticity in social tolerances likely precludes spacing behavior as a plausible mechanism regulating population densities. Male social behavior was more complex than previously described for northern populations, with most adults forming a coalition group with conspecifics. Male coalition groups formed despite the finding that females were regularly spaced, which contradicts working hypotheses for mechanisms of grouping behavior in male carnivores. I propose that group formation was likely due to the benefits that dominant males received through increased efficiency in territory maintenance and the increased likelihood of territory inheritance by subordinate males.

5.1 LITERATURE CITED

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APPENDIX A. CONDITION INDICES AND BIOELECTRICAL IMPEDANCE ANALYSIS TO PREDICT BODY CONDITION OF SMALL CARNIVORES: A TEST WITH RACCOONS

A.1 INTRODUCTION

The ability to acquire and store energy reserves is a basic component of mammalian populations. Understanding nutritional condition and how it relates to demographic processes is an important component of animal ecology (Virgl and Messier 1992). In general, individuals with greater energy reserves enjoy higher rates of survival, reproduction, and ultimately higher genetic fitness (Millar and Hickling 1990; Hodges et al. 1999; Milner et al. 2003). Many ecological parameters may influence body condition, including food availability, weather, and space-use (Millar and Hickling 1990; Winstanely et al. 1999; Revilla and Palomares 2002). Several other inherent qualities may also influence condition such as the ability to defend territories, store body fat, or select favorable den sites. The capability to accurately estimate body condition may allow us to quantify these variables into a single metric (Speakman 2001); however, determining body condition of individuals in wild populations has been a continual challenge for ecologists to accurately measure (Green 2001).

For our purposes, body composition is defined as the ingesta-free components of water, protein, ash, and/or mineral of an individual (Robbins 1993); while body condition refers to an animal's energetic state and is a measure of the variation of body fat (measured as percent body fat--Shulte-Hostedde et al. 2001; Speakman 2001). Several

methods have been developed to assess body condition of wild animals, which generally fall into two categories: direct vs. indirect measures (Speakman 2001).

Direct analysis quantifies the amount of stored lipids and lean dry mass by chemically extracting fats from a ground homogenate that has been dried to remove body water (Reynolds and Kunz 2001). Direct analysis of whole carcasses is the most accurate way to assess body composition (Speakman 2001); however, this method is time consuming, expensive, and inappropriate when populations are too small to warrant such an analysis. Furthermore, since direct analysis requires destruction of the individual, it eliminates the ability to conduct longitudinal studies and precludes researchers from linking present condition with future fitness performance. As an alternative, ecologists have developed several non-destructive or indirect methods of estimating body condition.

Morphometric condition indices based on a metric of structural size and mass have been used pervasively as a means to non-intrusively assess body condition. The underlying assumption is that the mass of an animal, once corrected for structural size, should reflect stored energy reserves (Jakob et al. 1996). These morphometric indices are used commonly even though there has been little supportive evidence that they provide meaningful estimates that relate to body condition (Green 2001). Three morphometric indices (and slight modifications there of) are generally used to indirectly assess body condition: the ratio index, slope-adjusted ratio index, and the residual index (Krebs and Singleton 1993; Jakob et al. 1996; Hwang et al. 2005). In order to ensure these methods provide meaningful estimates, their accuracy and precision need to be examined (Cattet et al. 1997). However, validation of morphometric indices has rarely been completed, especially for carnivores (Huot et al. 1995).

The use of conductive methods have recently become recognized as a quick, non-intrusive, and inexpensive means of estimating body condition in mammals (Speakman 2001). Bioelectrical impedance analysis (hereafter BIA) relies on the properties of biological tissues and their varying electrical properties (Kushner 1992). An impedance plyethysmograph (often called BIA machine) is used to measure the resistance of a low level current which reflects body water and lean dry mass. The general principle of BIA is that the impedance of a geometrical isotropic conductor is related to its length and shape given a constant signal frequency (Kushner 1992). In order to estimate body fat, users rely on a tight inverse relationship between total body fat and total body water. Further details of the principles and applications of BIA are given by Kushner (1992) and Van Marken Lichtenbelt (2001).

Raccoons (*Procyon lotor*) are a relatively recent invader to the Canadian prairies and parklands and undergo periods of dormancy during winter months (Larivière 2004). In preparation for winter dormancy, raccoons store large amounts of fat which is diminished by spring emergence (Mech 1968). As a consequence, raccoons at the northern edge of their range distribution may experience body mass fluctuations of up to 40% of their original mass (Mech 1968); which makes them good candidates for examining the usefulness of various techniques used to estimate body condition. I was interested in testing the ability of these standard morphometric condition indices to predict body condition in raccoons as well as test the ability of BIA to generate models of body condition.

Additionally, when generating models to predict body condition using conductive methods, it is generally thought to require species specific models rather then using

general morphological equations (Unangst and Wunder 2001). The general 'morph hypothesis' predicts that when estimating body condition of animals that are of similar size and life history characteristics, a general morphological equation should be sufficient to estimate this parameter (Unangst and Wunder 2001). This hypothesis stemmed originally from another conductive method of estimating body condition, total electrical body conductivity (TOBEC). One of the manufacturers of small animal composition analyzers, EM-SCAN (EM-SCAN Inc., Springfield, Illinois, USA), provides users with a general morphological equation developed from laboratory rats. The equation has generally been used for small mammals when validation and species specific models have not been derived. However, there are few cases where studies have been able to compare models generated for relatively similar species using conductive methods, and none which compare general morph equations for carnivores using BIA. I report on 1) the ability and resolution of 3 morphometric indices and BIA to estimate body condition of raccoons and 2) test the 'morph hypothesis' presented by Unangst and Wuner (2001) to assess the need for species specific models to predict body condition using BIA through a comparison of other predictive equations recently published by Hwang et al. (2005).

A.2 MATERIAL AND METHODS

A.2.1 *Capture and handling*

Thirty-three raccoons (17F, 16M) were captured in the prairie parkland region of Manitoba, near Minnedosa (50° 14′ N, 99° 50′ W) from April to November, 2003. Trapping spanned from early spring to late autumn in an effort to include a representative

sample of varying body conditions. Raccoons were captured in commercial, mesh-wire live traps (12 in x 12 in x 36 in--Billman Supplies, Columbus, Ohio, USA) that were checked each morning as raccoons are primarily nocturnal (Greenwood et al., 1982). To facilitate handling, captured raccoons were anesthetized using a standard dose of 20 mg of Zoletil® by an intramuscular injection to the hind leg (Pitt et al. 2005). Following anesthesia, captured raccoons were aged, sexed, and ear-tagged (National Wing Bands, Newport, Kentucky, USA) to replicate normal handling procedures. Raccoons were weighed to the nearest gram using a Pesola spring-scale (Pesola Ag, Baar, Switzerland) to obtain total body mass (TBM).

I recorded a variety of morphological measurements (in mm), including: snout to vent (SVL), snout to tail (TOT), chest circumference (CC), and right hind foot length (RHF). Snout to vent length was measured from the tip of the snout to the vent; TOT was measured the same as SVL except measurement was extended to tip of tail bone. Chest circumference was measured as the circumference of the chest immediately posterior to the front appendages. I measured RHF as the length of the foot pad (excluding digits) using a digital caliper.

Impedance was measured using a portable plethysmograph which read from 0-10000 ohms with a resolution of 1 ohm and accuracy of $\pm$ 0.5% (BIA machine; model 101A, RJL Systems, Detroit, Michigan, USA). All raccoons were place sternally recumbent on a non-conductive surface. Electrodes were attached to the upper lip at the canines using alligator tips as conductors and at the base of the tail. Resistance (R_c) and reactance (X_c) values were recorded after readings stabilized and until two readings fell within 5% of each other, which were then averaged following Hwang et al. (2005). After

completion of field handling, raccoons were immediately euthanized by a cardiac injection of T-61® (0.3 ml/kg, Hoechst Animal Health, Beneflux, Belgium). Raccoons were triple wrapped and stored frozen at -20°C to prevent loss of water until ready for dissection.

A.2.2 *Chemical analysis*

Raccoons were skinned and fleshed to remove fat. Carcass and internal organs were also dissected of fat which was then weighed to the nearest gram. All ingested material was removed from gastrointestinal tracts. Raccoons (including viscera, dissected fat, ingesta-free carcass, and pelt) were then ground into a homogenate using an industrial meat grinder (Model 84186, Hobart Inc., Troy, Ohio, USA) and the resulting mixture was used for direct chemical analysis. I used 200 g aliquot sub-samples from each homogenate to determine total body water (TBW). Samples were placed in a drying oven at 90° C for 7 days to ensure complete loss of water (Kerr et al. 1982). Samples were then ground and an aliquot 10 g sub-sample was used for all further chemical analysis. Samples were placed in thimbles and lipids were extracted in a Soxhlet apparatus using petroleum ether (Dobush et al. 1985) which left lean dry mass (LDM).

A.2.3 *Statistical analyses*

I tested three condition indices: the ratio index, slope-adjusted index, and the residual index. Indices were calculated as follows: (1) The ratio index was calculated as body mass (kg) divided by body length (SVL was used for length in all calculations of indices). Two variants of this index were also used: body mass divided by body length with body length raised to the powers of two and three to represent the pretense that mass and linear measurements increase isometrically (Cone 1989). (2) The slope-adjusted index was

calculated by dividing body mass by body length, with body length raised to the slope of the ln-transformed mass to ln-transformed length regression (Jakob et al. 1996). (3) Residual index was calculated by dividing ln-transformed body mass and ln-transformed length and then examining the usefulness of the residuals in predicting total body fat. I used ordinary least square (OLS) linear regression to assess the ability of condition indices to predict total body fat (Schulte-Hostedde et al. 2005).

Bioelectrical impedance analysis was used to assess if reactance and resistance values could improve on the ability of structural measurements to predict body condition. Resistance is equal to the opposition of flow to an alternating current; while reactance is equal to the opposition of flow to electric current caused by tissue and cell membranes (Kushner 1992). Resistance (R_s) and reactance (X_c) values determined by the BIA machine were used to calculate impedance (Z):

[1] $Z = (R_s^2 + X_c^2)^{0.5}$

With a constant electrical signal frequency and consistent configuration, impedance is related to the volume of the conductor (Kushner 1992; Bowen et al. 1999), meaning volume is equal to the length (SVL) squared divided by the impedance. Since the size of the reactance is small compared to the resistance it has been common practice to substitute resistance for impedance (Bowen et al. 1999; Kushner 1992; Hwang et al. 2005), which gives the following equation:

[2] $\text{Volume} = L^2 / R_s$

Backwards stepwise regression was used to generate predictive equations for TBW and LDM. Variables made available for inclusion in the model included: SVL, CC, RHF, TBM, Z, L^2/R_s, TBM/SVL, TBM/$SVL^{2, 3, \text{ and } 2.447}$, and the residual index.

Equations developed to estimate TBW and LDM were used to estimate total body fat (TBF) using the following equation:

[3] TBF = TBM - TBW - LDM

Simple linear regression was used to compare the estimates of TBW, LDM, and TBF with those of the chemically derived values. Coefficients and standard error of the estimates (SEE) were used to compare predictive equations (Bowen et al. 1999). Akaike's Information Criteria (AIC) was used to examine the usefulness of all models generated to predict TBF (Burnham and Anderson 1998).

Predictive equations developed to estimate body condition of striped skunks in Saskatchewan (Hwang et al. 2005) were used to predict TBW, LDM, and TBF in raccoons to determine how accurately these models could predict TBF in a similar species inhabiting a similar environment to address if there is a need to develop species specific models. Equations used from Hwang et al. (2005) are:

[4] $TBW = -1.1 + 0.058 (CC) + 0.25 (L^2/R_s)$

[5] LDM = 0.26 + 0.12 (TBM)

Total body fat was then determined by using equation 3. I compared estimates of total body fat with those of the chemically derived values using linear regression as above.

A.3 RESULTS

The mass of raccoons ranged from 1.6 to 12.3 kg ($\bar{x}$ = 6.1, SD = 3.1, n = 33), with body fat ranging from 3-30% as determined by direct chemical analysis. Absolute values of body fat ranged from 0.1-3.0 kg ($\bar{x}$ = 0.95, SD = 0.71, n = 33). Dissectible fat from whole carcasses correlated well with the estimates provided by direct chemical analysis

(r^2 = 0.97, SEE = 0.16, P < 0.001), indicating the majority of fat reserves were subcutaneous and around major organs.

A.3.1 *Morphometric indices*

In general, morphometric indices were poor estimators of body condition, with the best model being the modified ratio index in which body length is raised to the power of two. Albeit the best, this index explained only 62% of the observed variation in body fat (r^2 = 0.62, SEE = 0.52, P < 0.001; Table A.1). The residual index, which may be one of the more popular indices for mammals, was one of the lower ranking models for raccoons (Table 1, 2). I regressed ln-transformed body mass on body length and used the slope of that line as the exponent in the slope-adjusted ratio (y = -16.1 + 2.77x), which also performed poorly in estimating fat reserves (r^2 = 0.10, SEE = 0.37, P = 0.03). The best morphometric model only carried 0.023 in Akaike weight, and all morphometric models combined carried only 0.084 (Table A.2).

Table A.1. Results from OLS multiple and simple linear regressions between condition indices, BIA values, morphometrics, and total body fat as derived from chemical analysis for 33 raccoons collected in Manitoba, Canada, 2003. The general morph model (skunk model) was adapted from Hwang et al. (2005). For all equations, mass is measured in kg and length measured in mm.

Condition Indices	Predictive Equation	r^2	SEE
Ratio	TBF = -0.56 + 139.8(mass/length)	0.56	0.67
Modified Ratio	TBF = -1.649 + 151043(mass/length^2)	0.62	0.52
Modified Ratio	TBF = -1.472 + 81488473(mass/length^3)	0.16	0.62
Slope-adjusted	TBF = 0.926 + -129799(mass/length$^{2.77}$)	0.10	0.37
Residual Index	TBF = -0.259 + 0.591(residual)	0.31	0.57
BIA			
Total Body Water	TBW = -0.165 + 0.488(TBM) + 0.001 (L^2/R_s)	0.99	0.20
Lean Dry Mass	LDM = -0.94 + 0.002(SVL) + 0.001(L^2/R_s) + 0.098(TBM)	0.96	0.15
Total Body Fat	TBF = TBM - TBW - LDM	0.94	0.16
Skunk Model			
Total Body Water	TBW = -1.1 + 0.058(CC) + 0.25(L^2/R_s)	0.91	0.34
Lean Dry Mass	LDM = 0.26 + 0.12(TBM)	0.87	0.13
Total Body Fat	TBF = TBM - TBW - LDM	0.69	0.78

A.3.2 *Bioelectrical impedance analysis*

Total body water was estimated using backwards stepwise regression. Total body mass and bioelectrical volume were the best predictors of TBW (Equation 6):

[6] $TBW = -0.165 + 0.488(TBM) + 0.001(L^2/R_s)$

Predicted values for TBW from equation 6 correlated well with values derived from direct chemical analysis ($r^2 = 0.99$, SEE = 0.20, $P < 0.001$). I then followed the same procedure to develop a model for LDM estimation. Bioelectrical volume, TBM, and SVL were the best predictors:

[7] $LDM = -0.939 + 0.002(SVL) + 0.001(L^2/R_s) + 0.098\ (TBM)$

Predicted values as obtained through equation 7 corresponded well with values calculated through direct chemical analysis ($r^2 = 0.96$, SEE = 0.15). Total body fat was then calculated by subtracting the estimates of TBW and LDM from TBM to get TBF using equation 3. Total body fat estimates also correlated well with the values derived by direct chemical analysis ($r^2 = 0.94$, SEE = 0.16, $P < 0.001$). Bioelectrical volume, along with body mass and body length, were important variables in estimating total body fat and combined in the top three models to carry 0.77 of Akaike weight (Table A.2).

Table A.2. Akaikie's Information Criteria (AIC) selection and ranking of models used to predict total body fat for 33 raccoons from Manitoba, Canada 2003. Variables made available for inclusion of models were: total body mass (TBM), chest circumference (CC), length, right hind foot (RHF), snout to vent length (SVL), L^2/R_s, impedance (Z), and morphometric indices.

Model	K	AIC_c	Δ AIC_c	ω_i	Rank
TBM, L^2/R_s	4	2.52	0.0	0.48	1
TBM, SVL, L2/Rs	5	4.65	2.1	0.17	2
TBM, Z	4	5.29	2.8	0.12	3
TBM, L^2/R_s, CC	5	5.42	2.9	0.11	4
TBM, RHF, CC, L^2/R_s	6	8.20	5.7	0.028	5
Modified Ratio (TBM/SVL^2)	3	8.56	6.1	0.023	6
Ratio Index	3	8.85	6.3	0.020	7
Residual	3	9.21	6.7	0.017	8
Slope Adjusted	3	9.84	7.3	0.012	9
Modified Ratio (TBM/SVL^3)	3	10.13	7.6	0.011	10
TBM, L^2/R_s, SVL, CC, RHF	7	11.27	8.8	0.006	11
TBM, Z, SVL, CC	6	14.87	12.3	0.001	12

A.3.3 *General morphological equation*

Equations 4 and 5 developed for striped skunks performed relatively well in their ability to predict TBW and LDM in raccoons. Regression analysis explained 91% of variation observed in TBW, but had a relatively higher SEE (0.34). Accuracy for LDM estimates were similar to TBW, with $r^2 = 0.87$ (SEE = 0.13). Total body fat as estimated through LDM and TBW however performed substantially poorer when compared to models derived specifically for raccoons ($r^2 = 0.69$, SEE = 0.78, $P < 0.001$--see table 1), but did perform better than morphometric indices. Typically, estimates provided by the general morphological model over estimated total body fat in raccoons with total body fat estimates as high as 56% and total body fat averaging 36% for all individuals.

A.4 DISCUSSION

There is an increasing interest in longitudinal studies that relate body condition and animal ecology (Speakman 2001). The ability to obtain reliable estimates of body condition is an important component to the investigation of how this variable relates to ecological factors. Using data from raccoons across seasons and with a wide range of physical conditions, I demonstrated that morphological condition indices alone are unsatisfactory to estimate body condition in raccoons, with the best model explaining only 62% of the variation observed in total body fat. Moreover, the residual index is one of the more popular condition indices used by ecologists. However it was among the poorest in terms of explanatory capability, had high standard errors of the estimate ($r^2 =$ 0.31, SEE 0.57), and ranked low in AIC model selection. These results add to the growing body of literature that suggests morphometric condition indices alone have a

relatively low capability of predicting body condition in carnivores (Cattet 1990; Huot 1995; Winstanely et al. 1998; Hwang et al. 2005).

In contrast to the low explanatory ability of indirect methods, bioelectrical impedance analysis provided a simple yet reliable estimation of total body water and lean dry mass. From these equations, I was able to predict total body fat in raccoons. A combination of resistance values and morphometric measurements were able to explain 94% of the variation of observed total body fat and had relatively low standard errors of the estimate. Impedance values along with standard measurements of body length and body mass were selected for use in our stepwise regression analysis. During this study I established the ability to repeatedly assess body condition over a longitudinal study in a non-intrusive manner.

My results do not support the morph hypothesis and suggest that independent species-specific models should be derived to provide estimates of total body fat. Equations furnished for striped skunks performed substantially poorer than the models derived specifically for raccoons; and generally over-estimated total body fat. Striped skunks, as derived through direct chemical analysis, had fat stores that exceeded more than 50% of total body mass with total body fat exceeding 3 kg in absolute value (Hwang et al. 2005). In contrast, the maximum percentage of total body fat observed in raccoons was 30% of the total body mass and rarely exceeded 3 kg in absolute value. Differences in life history, especially over-wintering strategies and the capability to store body fat, may explain why the general morphological model performed poorly when compared to the species-specific model. In instances where it is impossible or difficult to validate an independent model, the equations furnished by a similar morph appear to provide more

accurate estimates of body condition compared to species-specific morphometric condition indices. However, morphological and physiological differences between skunks and raccoons may have been too great to provide estimates with the accuracy comparable to a species specific model. Further testing of this hypothesis with species that are more similar may provide more accurate estimates and is an area warranting further research.

Body condition is a difficult parameter to estimate; however, conductive methods show remarkable ability to predict body condition and composition across wide taxa of species (Farley and Robbins 1994; Bowen et al. 1999; Hundertmark and Schwartz 2002; Hwang et al. 2005). A move away from the use of morphometric condition indices would greatly increase the inference of ecological studies and would put to rest remaining uncertainties and criticisms (Green 2001; Hayes and Shonkwiler 2001). In this study, bioelectrical impedance analysis provided quick and reliable estimates of body condition and its utility in field studies should continue to grow.

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